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Errata

Page 238, paragraph 2, see correction paragraph on page 553.
Page 259, line 5, for '*eugenics*' read '*genetics.*'
Page 261, next to last line, for '*2 August 1928*' read '*12 July 1928.*'
Page 419, line 13, for '*P. scarioas*' read '*P. scariosa.*'

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Sex ratio and chromosomes in Riccia Curtisii

FREDERICK MCALLISTER

(WITH ELEVEN TEXT FIGURES)

The adherent spore tetrads of *Thallocarpus Curtisii* Lindb. seem to have unduly influenced Austin (3, 4) and Lindberg (13) to place it with the Sphaerocarpales. Schiffner (17) in Die Natürlichen Pflanzenfamilien follows their lead in placing *Thallocarpus* close to *Sphaerocarpos*. Adherent spore tetrads are not peculiar to the Sphaerocarpales, for in *Sphaerocarpos cristatus* M. A. Howe the spores of the tetrad separate long before maturity. Those of *S. Donnellii* Austin separate at maturity. On the other hand the spores of *Riccia synspora* Schiffner (18) adhere tenaciously in spore balls. There seems little reason for excluding *Thallocarpus* from the Ricciaceae. Howe (11) in his recent revision of the genus in North American Flora, has included it with the Ricciaceae as *Riccia Curtisii* T. P. James. Howe's usage will be followed in this paper.

In these forms with adherent tetrads the dissemination of the spores is mainly in fours. The subsequent germination tends to give rise to a compact group of four plants, the product of a single spore mother cell. Since the sex of the resulting gametophytes is recognizable in very young plants, often when they are less than 0.5 mm. in diameter, these forms have been regarded as especially favorable for study of sex inheritance in the gametophytes.

Strasburger (21) recognizing the importance of these attached tetrads in the question of sex determination in *Sphaerocarpos*, made attempts to grow the plants from spores. *Sphaerocarpos terrestris* material obtained from Italy was discarded in favor of *S. Californicus* because of the larger size of the spore balls in the latter. Material of this latter species was obtained from near Chartres, first through the kindness of Ch. Douin, and later by Strasburger himself with the help of Douin. Attempts at growing the plants in the greenhouse were however unsuccessful, and Douin's further coöperation was sought. Douin (7)

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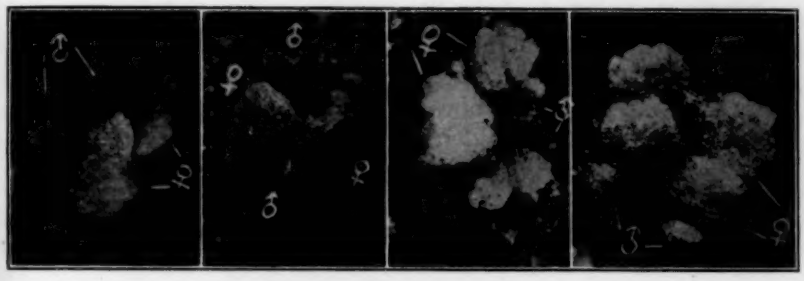
made careful examination of plants growing in the field and published his findings on 81 groups, each presumably having arisen from a single spore ball. Over half of the groups observed were made up of four plants, two of which were male and two female. The other groups could be explained as conforming to this proportion, as groups of four males and four females, or two females and two sterile plants, or two females and one male and one sterile plant. In no case were three plants of one sex and one of the other observed.

Under favorable cultural conditions, which however are rarely present in the field, *Sphaerocarpos* gametophytes are known to live for long periods. C. and R. Douin (8) grew plants of *S. terrestris* and *S. Californicus* for nine or ten months. Goebel (10) reports female plants as having grown for two years. Allen (2) found that female plants of *S. Donnellii* and *S. Texanus* could probably be kept growing indefinitely. Allen regards the possibility of vegetative propagation, due to the long life of the plants, as introducing a serious objection to data on sex distribution from field grown plants. He has germinated spore balls of *S. Donnellii* on a sterile substratum consisting of filter paper moistened with a nutrient solution as used by E. and E. Marchal (15) in culturing mosses. After germination the sporelings were each transferred to a separate pot of soil. The results were inconclusive because of the low percentage of germinations and the sterility of a considerable number of the plants secured. Data for one culture only were published and these showed that less than 43 per cent of the spores germinated, and of this 43 per cent, 30 per cent gave rise to sterile plants. Other cultures gave less satisfactory results. Unless better germination and maturing of the spores can be secured, data from the field must be regarded as more satisfactory. As a matter of fact growth conditions in the field, at least in Texas, are not conducive to long life of plants of *Sphaerocarpos* or *Thallocarpus*. The plants are very easily killed by drying or freezing, having none of the resistance to these conditions that most leafy liverworts and many mosses have. If plants are observed as soon after germination as the sex can be recognized there is no chance for vegetative propagation.

In another connection attention has been called to the probability that in *Riccia Curtisii* the four spores of the tetrad

seem to give rise to two male and two female plants. It is the aim of this paper to present further data on this point as well as evidence on the dioecism of the gametophytes. Observations on the chromosome equipment in the nuclei of the two sexes will also be presented.

In *R. Curtisii*, as in other Riccias, the archegonia are entirely imbedded and hidden in the thallus, and never show any external associated structures such as the involucre-like outgrowths in *Oxymitra* or *Corsinia*. The male plants are, however, recognizable quite early. As the antheridia approach maturity their presence is indicated by slender cylindrical tips of the ostioles protruding above the surface of the thallus as shown in figures 1 and 3. After the maturity of the antheridia and the escape of the



1 2 3 4

FIG. 1. RICCIA CURTISII. A group of four plants. One female plant overlapping the other. Ostioles showing at surface of male plants. FIG. 2. A group of four plants, older than those of fig. 1. Two male plants with darkened center. The female plants had nearly mature sporophytes. FIG. 3. Four plants. One of females deeply lobed. Male plants have ceased growth while females are continuing growth. Ostioles conspicuous. FIG. 4. An older group of four, the two female plants overlapping and conspicuously lobed. The male plants are about the size of those in fig. 1. while the females are many times larger and with mature sporophytes. (All × 7.5, slightly reduced in reproduction.)

sperms, the central region of the male thallus takes on a reddish-brown color (FIG. 2). The female plants do not show this discoloration. This coloration was helpful in preliminary examinations of plants upon which ostioles were not readily recognized. By the time the male plants show this characteristic color, many

of the female plants will be found, upon dissection, to contain sporophytes, which, of course, affords a very satisfactory evidence of their sex.

In many doubtful cases of the sex of members of groups of four, the plants were imbedded in paraffin and sectioned. A study of the morphology of *R. Curtisii* (McAllister, 14) necessitated the sectioning of many gametophytes which were made available for this study. Later studies on the chromosome equipment of the nuclei of the two sexes have necessitated the sectioning of many more gametophytes. A considerable number of these were groups of four plants, kept separate and examined carefully as to the sex. A number of doubtful cases, sometimes involving sterile plants, were dealt with this way.

In the examination of sections, the question as to whether *Riccia Curtisii* is strictly dioecious has always been kept in mind. Of course, in the *Riccia* type of thallus, the only sure evidence of strict dioeciousness would be from serial sections. Approximately 110 plants were sectioned and examined, and in no case was there any evidence of both archegonia and antheridia in the same plant. As far as my observations go, *R. Curtisii* is strictly dioecious.

Attempts to grow mature gametophytes for extended periods to demonstrate the permanence of sex have not as yet met with success. The extreme heat of Texas summers, together with high humidity necessary for the growth of these plants, is so favorable for the growth of terrestrial blue green algae that most thallose plants are soon smothered out. It is quite possible that female plants of *Riccia Curtisii* would grow for extended periods in regions where the temperature can be kept low enough.

Repeated attempts to grow the gametophytes from spores in the greenhouse have met with little success. Only a small proportion of the spores germinate. Many of the sporelings obtained are overgrown by blue green algae and fungi and destroyed before the sex can be determined, so that but a small percentage reach maturity.

Plants grown in the field naturally show considerable irregularity of distribution, tending to be massed in groups of from 2 to 20 plants. The large groups are obviously of little value in determining the sex of plants resulting from the spore balls. There are, however, many isolated smaller groups to be seen,

and it is to these that most of our attention has been directed. Groups of less than three plants were not recorded, nor were records made of groups which were not well isolated from other plants. No group was considered unless the plants comprising it were close together. The larger groups were avoided, since evidence from them could obviously not be as definite and clear cut as from groups of four or three. Young plants were used, as soon as feasible after germination, to eliminate as far as possible chance of vegetative propagation.

About half of the groups recorded were sectioned in paraffin. Many others were carefully dissected. In the latter part of the study, after the author had become convinced of the strict separation of the sexes in the gametophyte, the presence of sporophytes was regarded as sufficient evidence to prove femaleness, and the presence of ostioles as showing male plants. The labor of determining the sex of these minute plants with certainty has limited the author to what may seem to be a small number of groups. It should not be forgotten, however, that 240 plants were involved.

Attention should be called to the importance of the early maturity of these gametophytes in a study of sex distribution. Male plants with mature antheridia are often but slightly more than one millimeter in diameter (FIGS. 1–4), while female plants of two millimeters in diameter are often found with sporophytes approaching maturity (FIGS. 1, 2). No outdoor data as to the exact age of such minute plants is available. Dry periods in winter often cause the death of *Riccia Curtisii*, yet plants with mature sex organs are to be found within two weeks after such dry periods are broken by moist weather. Probably most plants mature within two or three weeks. Obviously there is less chance for the destruction of part or all of the plants by drouth, insects, or other agencies, and less chance for a possible multiplication of plants by vegetative propagation with these plants than with gametophytes requiring several months for maturing.

The rate of growth of the male and female plants seems at first to be about the same, for in very young groups all of the plants are alike in size and appearance. Later the male plants practically cease growth in nearly all cases, while the female plants continue to grow rapidly for some time longer, so that at the maturity of the sex organs the female is usually at least

twice as large as the male (FIGS. 1, 2). After fertilization the male plant usually ceases growth entirely while the female continues to grow for a period (FIGS. 3, 4) so that the former are often entirely overgrown and covered by the latter.

In all 61 groups of plants were examined sufficiently for record. The composition of these groups is shown in the following table:

36 groups:	2 female plants,	2 male plants	
8 groups:	2 female plants,	1 male plant	
6 groups:	1 female plant,	2 male plants	
1 group:	4 female plants,	4 male plants	
2 groups:	4 female plants,	3 male plants	
3 groups:	2 female plants,	1 male plant,	1 sterile plant
4 groups:	2 female plants,	0 male plants,	2 sterile plants
1 group:	1 female plant,	1 male plant,	2 sterile plants

Nearly two-thirds of the groups examined show two male and two female plants. The remaining groups can be explained as conforming to this proportion: the groups of three plants either lack a female or a male plant, and are never made up of three males or three females; the large groups of seven or eight plants were obviously from two tetrads. This evidence makes it a reasonable conclusion that in those cases where sterile plants form a part of a group of four, they represent the plant or plants of either sex lacking to make up the two and two proportion. Thus, in those plants with two females and one male and one sterile plant, the sterile plant is a male which, from some physiological cause has failed to produce antheridia.

There seems no doubt that in *Riccia Curtisii* the four spores of the tetrad regularly give rise to two female and two male plants. That the separation of the two sexes, which were united in fertilization, takes place during the reduction divisions seems to be an obvious further conclusion.

Allen (1) has described a difference in the chromosome equipment of the male and female plants of *Sphaerocarpos Donnellii*. One of the eight chromosomes of the nucleus of the female plant is very much larger than any of the others. No chromosome comparable to this large one is recognized in the male gametophyte. 'Seven of the eight chromosomes of the male, varying in length among themselves, seem to correspond to the seven smaller ones of the female. The eighth chromo-

some is very small.' This small chromosome is regarded by Allen as corresponding to or replacing the large one in the female. He designates the large chromosome as the *X* chromosome and the small one of the male as the *Y* chromosome. Studies on the sporophyte nuclei reveal but 15 chromosomes. The large chromosome is always recognizable. The small one is regarded as either hidden, or invisible because of lack of sufficient stain. The minuteness of the small nuclei makes them very difficult to study, as is evidenced by the extreme magnifications used. Although all the figures are small, the magnification is 3800. Due to this extreme magnification the differences in the size of the smaller chromosomes are difficult to judge.

Miss Schacke (16) has reported that a similar chromosome difference exists in the nuclei of the male and female gametophytes of *Sphaerocarpos Texanus*. No figures are given.

Showalter (19, 20) working in Allen's laboratory, has studied the chromosomes of the male and female gametophytes of *Conocephalum conicum* and *Riccardia pinguis* in order to determine whether a difference exists in the two sexes. His results were negative with both species. No perceptible difference could be observed between the chromosomes of the two sexes in either species.

Allen (2) suggests that the large chromosome in female plants of *Sphaerocarpos* may be correlated with the larger and more rapid growth size of the female gametophyte. Since *Riccia Curtisii* shows strict separation of sexes, as well as a marked distinction in the rate of growth and the size of the male and female plants at maturity, the chromosome equipment of the two sexes is of especial interest.

Numerous dividing nuclei of cells of *R. Curtisii* have been studied and drawn. A few of these have been selected for illustrations.

The nuclei and chromosomes are very small, apparently somewhat similar in size to those of *Sphaerocarpos*. The chromosome number is eight in both male and female nuclei (FIGS. 5–8). The chromosomes differ among themselves in size, but these differences seem to be the same in both male and female nuclei. A single chromosome, noticeably smaller than the rest, is present in the nuclei of both male and female plants. Two large chromosomes, approximately straight, two, somewhat smaller,

having a tendency to be curved or hooked, and three medium sized rod-like chromosomes are usually to be recognized in all gametophytic nuclei of suitable age and orientation.

In the sporophyte (FIGS. 9, 10), the nuclei have sixteen chromosomes. Two small chromosomes are to be seen in all suitable nuclear figures of the sporophyte, and the duplication of the other chromosomes seems to be obvious. In the heterotypic

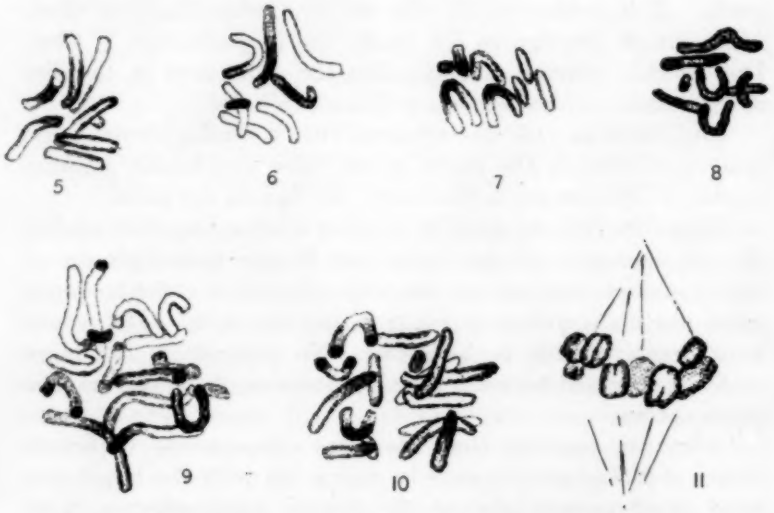


FIG. 5. Chromosome group from wall of young antheridium. FIG. 6. From interior cell of very young antheridium. FIG. 7. Chromosome group from venter wall of young archegonium. FIG. 8. Group from apical region of female gametophyte. FIG. 9. Group from wall of young sporophyte. FIG. 10. Group from interior of immature sporophyte. FIG. 11. Heterotypic metaphase of *Riccia Curtisii*. (All × 3500.)

metaphase (FIG. 11) eight pairs of chromosomes are to be observed with one pair much smaller than the rest. Here, due to the excessive shortening and thickening during this phase, the differences between the chromosomes are not so noticeable.

Slight differences are to be observed in the apparent size of chromosomes in the different nuclei, as will be observed by an examination of the drawings. These fluctuations are slight and are not constant. They are undoubtedly due to differences in the orientation of nuclei and chromosomes. No definite and

constant difference has been observed between the chromosomes of the two sexes.

Beer (5) found seven or eight chromosomes in the gametophyte of *Riccia glauca*. Miss Black (6) found eight in *Riccia Frostii*. On the other hand Garber (9) reported four chromosomes for the gametophyte of *Riccia lutescens*, and Lewis (12) found four chromosomes in the gametophytes of *Riccia crystallina* and *Riccia fluitans*. In all of these cases reference to chromosome number was largely incidental and no mention was made of the size and form of the chromosomes.

It seems apparent that, since sex segregation in *Sphaerocarpos* and *Riccia Curtisii*, and probably in other dioecious Bryophytes, takes place at the time of the reduction divisions, it must be determined by the distribution of the chromosomes. It is also clear that visible chromosome differences such as *X* and *Y* chromosomes are not necessarily concerned with sex segregation, since such chromosomes are lacking from the nuclear equipment of *Conocephalum*, *Riccardia* and *Riccia Curtisii*, all of which show strict separation of sexes.

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Nuclear and cell division in the antheridial filaments of the Characeae

JOHN S. KARLING

(WITH PLATE 1)

The antheridial filaments of the Characeae are unusually favorable for study of extended series of nuclear and cell division stages in growing tissues. The number of filaments in an antheridium may often be as high as two hundred, and, since each filament consists of an average of about seventy-five cells, a single antheridium may contain as many as fifteen to twenty thousand cells in separate linear series. The cells of these filaments are free from chloroplasts, other pigment bodies, and stored foods; and the ratio of the diameter of the nuclei to the cell diameter is nearer 3 to 4 than 2 to 3, as Strasburger (1893) assumed was normal for embryonic cells. Long filaments may be frequently found in which as many as a hundred cells are undergoing division at the same time, and many of the series of changes involved in nuclear and cell division from the resting stage to the reorganization of the daughter nuclei and the formation of the new cell wall may often be seen in a single filament.

Since the time of the classical observation of Strasburger (1884a) of the series of nuclear division stages from one end of the embryo sac of *Fritillaria* to the other, synchronous or simultaneous nuclear division has been found to be of wide occurrence in multinucleate cells. The data relate chiefly to nuclear division in coenocytes, and little is known as to the time relations of the division stages in the nuclei in adjoining cells of multicellular tissues such as root tips and leaf and stem primordia. The literature dealing directly and indirectly with synchronism in nuclear division is extensive, especially in the field of animal embryology. I shall summarize only such data as have been related to the more general problems as to the nature of the division process.

In *Fritillaria imperialis*, as noted, Strasburger found a more or less regular but discontinuous succession of division stages, from early prophases in the micropylar region, to late telophases and daughter nuclei in the chalazal end of the embryo sac.

His observations have been confirmed by Heuser (1884) Sijpkens (1904) and Saame (1906). Soltwedel (1882) and Němec (1910) report many similar cases among the Angiosperms, but find that the succession of division stages may occur either from the micropylar to the chalazal end or vice versa. In *Corydalis pumila*, *Caltha palustris*, and *Urtica pilulifera* they report early division stages in the chlazal end with progressively older stages towards the micropyle, and in *Corydalis cava* and *Polygonum Bistorta* they find a series in reverse order. On the other hand, Hegelmaier (1884) found no longitudinal progression of division stages in the embryo sac of *Euphorbia Lathyris*. Nuclear division was found in girdle-like zones, while the nuclei in the surrounding region were in complete rest. In the Angiosperms the nuclear divisions in the megaspore which give rise to the eight-nucleate female gametophyte are also generally simultaneous. This is true also of the divisions in the female prothalli of *Selaginella* and the megasporangia of *Marsilia*, according to Lyon (1901) and Shattuck (1910).

In the proembryo of the Gymnosperms simultaneous nuclear division is of general occurrence, according to Ikeno (1898) Jäger (1899) Land (1902) Coulter and Chamberlain (1903) Miyake (1903) Coker (1907) Kildahl (1907) Lawson (1907, 1910) and Chamberlain (1910). Fertilization in this group of plants is generally immediately followed by a more or less long period of simultaneous free nuclear division. In *Dioon* Chamberlain reports that the ninth mitosis which gives rise to the 512-nucleate stage may occasionally be the last of the simultaneous divisions, but often a tenth mitosis follows which may give rise to 1024 free nuclei. In all of these cases the synchronously dividing nuclei are generally found to be in the same stage of division at any one time throughout the entire proembryo.

Other examples of simultaneous or synchronous nuclear division are found in the primordia of the vascular elements and in latex tubes, according to Treub (1880) Pirotta and Buscalioni (1898) Buscalioni (1898) and Němec (1910). In latex tubes Němec found that the early division stages begin in a definite region, 0.3 to 0.6 mm. from the apex of the tube which lies in that part of the surrounding vegetative tissue in which nuclear division is taking place most rapidly. From this region in both directions successively later stages of division are found.

In the multinucleate cells of fungi simultaneous nuclear division is almost universal. Lister (1893, 1911) Nawaschin (1899) Jahn (1904) Osburn (1911) and Kunkel (1915) in the Myxomycetes, Griggs (1909) Bally (1911) Barrett (1912) and Wager (1913) in the Chytridiales, Wager (1899) Stevens (1899, 1901 a, b) Miyake (1901) Ruhland (1903) and Davis (1903) in the Peronosporales, Harper (1895, 1897, 1899, 1900, 1905) Guilliermond (1903, 1904a, b, c) Faull (1904, 1912) Fraser (1908) Fraser and Welsford (1908) Carruthers (1911) Juel (1916, 1921) Sax (1918) Bagchee (1925) and Jones (1926) in the Ascomycetes, Sappin-Trouffy (1896) Juel (1898) Christman (1905, 1907) Fries (1911) Levine (1913) Kniep (1913) and Dodge and Gaiser (1926) in the Basidiomycetes, are but few of many who figure simultaneous nuclear division in sporangia, antheridia, oogonia, asci and basidia. In all of these cases the nuclei not only divide simultaneously but are also found to be in the same stage of division at any one time. On the other hand, in the sporangia of two Myxomycetes, *Trichia* and *Fuligo*, Strasburger (1884b) and Harper (1900) find some evidence of progression in the nuclear division stages.

In the coenocytic algae, Timberlake (1901) and Yamanouchi (1913) for *Hydrodictyon*, Lewis (1909) for *Griffithsia*, and Kurssanow (1911) for *Vaucheria* report more or less of a succession of division stages from one end of the cell to the other. Kurssanow's observations, however, are not in agreement with those of Schmitz (1879a, b, c) Strasburger (1880) Fairchild (1894) and Němec (1910). They report that the nuclei in the Siphonales generally divide independently of each other. In the antheridia and oogonia of *Fucus* Strasburger (1896) and Yamanouchi (1909) report a more or less complete synchronism in nuclear division.

The cytological data from the literature dealing directly and indirectly with the time relations of nuclear division in multinucleate cells suggest that these time relations may be considered as of two types. In the majority of coenocytes studied, the nuclei not only divide in general simultaneously but are usually found at any one time to be in the same stage of division throughout the entire cell. This type is characterized by *complete synchronism*, and is characteristic of nuclear division in sporangia, antheridia, oogonia, asci, and basidia of the majority

of fungi which have been studied cytologically. It is also generally characteristic of the divisions in the megaspore of the Angiosperms, proembryo of the Gymnosperms, and particularly in the early cleavage stages of the eggs of several groups of animals. On the other hand, in many large syncytia such as embryo sacs, the simultaneously dividing nuclei show a fairly well graded and progressive but generally discontinuous series of successive division stages from one end of the cell to the other. This type of simultaneous nuclear division is then characterized by *progressive synchronism*. It may include cases in which the seriation of division stages is discontinuous, but, nevertheless, progressive by groups of nuclei as well as by single nuclei in linear series. A group of nuclei in the same general late prophase stage, for instance, may be followed by another group in the equatorial plate stage, etc. The seriation is thus progressive but discontinuous. This type of synchronism is well illustrated in the embryo sac of *Fritillaria* and other Angiosperms as it has been described by Strasburger, Heuser, Soltwedel, Buscalioni, Saame and Němec.

As noted before, little attention has been given to the occurrence of synchronism in division between the cells of vegetative tissues. In rapidly growing tissues, such as root tips and primordia of stems and leaves, the nuclei of the individual cells generally divide more or less independently of each other. This is generally true in plant embryos as well. On the other hand, in the early cleavage stages of the fertilized eggs of echinoderms, gastropods, cephalopods, annelids, elasmobranchs, teleosts, reptiles, and birds, nuclear division is generally completely synchronous. In *Synapta*, for instance, complete synchronism in nuclear division may occur up to the 512-cell stage, according to Wilson (1925). Similarly, in the antheridial filaments of the Characeae a high degree of synchronism in division is shown by the nuclei of adjoining cells. This synchronism may either be complete throughout an entire filament, or progressive for longer or shorter distances by linear groups of cells. This is well illustrated in the figures of antheridial filaments of *Nitella* and *Chara* shown in plate 1.

These figures are microphotographs of aceto-carmine preparations taken from fifteen minutes to two hours after mounting. The bulging of the cells in most of the filaments is the result of

swelling due to the acetic acid. In making these preparations the antheridia were removed from the plant and mounted on a slide in a drop of aceto-carmine, as described in a previous paper (Karling 1926). The shield cells were then removed with fine steel needles and the antheridial filaments separated with as little injury as possible. As soon as the cover glass is added such mounts are ready for study. The slight pressure of the cover glass brings the filaments into much the same plane, so that segments of from ten to twenty cells, depending on the magnification used, may be found in focus.

The appearance of the nuclei in these filaments has of course been somewhat altered by the aceto-carmine solution. As has been shown in a previous paper (Karling 1926, *figs. 81–90*), the visible effect of the aceto-carmine solution is to bring out the nuclear boundary more clearly and to cause what appears to be an aggregation of the denser nuclear elements into larger and more clearly differentiated irregular dense shreds, bodies and strand-like aggregations. No attempt is made in this paper to describe the minute details of mitosis. I shall attempt to describe only the microscopically visible mass colloidal changes in the cells of the antheridial filaments as they grow and divide.

Protoplasm is obviously made up of systems within systems, thus constituting a so-called polyphase system. The common text-diagrams representing so-called typical cells show at least the following internal phase systems: plastids with starch grains and pyrenoids, nucleus with linin, chromatin granules and nuclear sap, vacuolated nucleoli, vacuoles containing salts and proteids, centrosomes composed of centriole and centrosphere, and perhaps Golgi apparatus and chondriosomes. The nucleus with its chromatin granules, linin, nucleoli, and chromosomes suspended or imbedded in the nuclear sap is a polyphase system in itself, besides being imbedded in the cytoplasm in which are starch grains, yolk spheres, Golgi bodies, chondriosomes, and vacuoles containing proteids, salts and lipoids in solution.

The chemistry of colloids, as far as it is at present developed, relates chiefly to simple two phase systems, and little consideration has been given to the occurrence of polyphase systems, or systems within a system such as found in protoplasm. Perhaps the nearest approach to such a system in unorganized colloids is Hardy's (1899) demonstration of secondary interior phases in

gelatin. Hardy found that if a portion of the hydrogel of gelatin-water-alcohol is cooled slowly a watery interior phase is formed in a continuum of denser gelatin. If the cooling is rapid a secondary system of small droplets may appear in either the internal or external phase, depending on the concentration of the gelatin in the whole mass. These droplets or particles may make chains which anastomose to form reticular structures, constituting a secondary interior phase.

Seifriz (1923, 1924a, b, 1926) has recently questioned the view that protoplasm is an emulsion on the basis of his observations that emulsions show no elasticity, while protoplasm is highly elastic and forms an irreversible coagulum when killed. By means of microdissection and centifuging, Chambers (1917, 1919) and Heilbrunn (1920) have attempted to show periodic changes from sol to gel, and vice versa, in the protoplasm of echinoderm eggs during division. At the time the spindle is fully formed, according to Chambers, the greater part of the cells is a gel. The cytoplasm becomes a sol as the astral radiations fade out, and at the same time the sphere liquid collects at the two poles of the nucleus. The formation of the amphiaster is accompanied by a reversal to the gel state. A return to the sol condition takes place in the equator of the cell as the nuclear spindle divides.

Heilbrunn finds that the viscosity reaches its height just before the spindle appears and diminishes immediately afterwards. He considers gelation a predominating factor in spindle formation, since if gelation is suppressed the mitotic figure does not form. Lister (1893) Ödquist (1922) and Zimmerman (1923) likewise find that viscosity is highest during mitosis.

The more or less non-vacuolated animal egg, with its suspended 'yolk spheres, microsomes and macrosomes' in an apparently homogeneous ground substance, has perhaps more resemblance to an emulsion than the generally highly vacuolated cytoplasm of the cell of the onion root tip. According to Wilson (1925), the cytoplasm of the full grown egg consists of closely crowded yolk spheres and various granules suspended in a continuous hyaloplasm, which has an aveolar or pseudo-alveolar appearance. Strasburger (1913) describes the cytoplasm of the vegetable cell as consisting of a more or less highly vacuolated clear ground substance in which are imbedded numerous bodies and granules of various sizes.

It is particularly with reference to thready, fiber-like and reticulated structures that the data of colloid chemistry are lacking and inadequate. Such structures are almost universal in fixed protoplasm, and Klebs (1888) Haberlandt (1888) Schwartz (1892) Knoll (1908) Lidforss (1908) Boresch (1914) and Lewis and Lewis (1914, 1915) report that they are of wide occurrence in living protoplasm as well. Their presence means that in addition to suspension, emulsions and foams, fibers and reticulated structures must be considered as a constituent of the protoplasmic colloidal system. While there are few experimental data concerning such structures in unorganized colloids the granular reticulated chains produce by Hardy (1899a) as secondary interior phases in gelatin, and also the net- and alveolar-like structures and simulcra of astral rays and spindles produced in coagulated albumen, gelatin, peptone, egg albumin, and other similar substances by Fischer (1899) and Hardy (1899b) show considerable resemblance to the reticulated structures in living and fixed protoplasm.

OBSERVATIONS

The great abundance of the division figures in young antheridial filaments of the Characeae is well illustrated in the group of filaments shown in figure 9. Series of at least six different stages in nuclear division are shown in the filament represented in figure 13. This figure shows a portion of a filament from a variety of *Chara coronata* which has fourteen chromosomes. The striking fact which is at once evident is that while, as noted, some six different stages are easily recognizable in this filament, the series of stages is by no means continuous. The first eight cells of the apical portion appear to be in very early prophase stages, and there is little difference, if any, in appearance between any of the nuclei. The next two nuclei, 9 and 10, however, show a marked difference in appearance and may be interpreted as later prophase stages. Nucleus number 11 shows the chromatin elements still more sharply differentiated. The increase in size and density, and perhaps decrease in number, of the dark elements in these nuclei is obviously an indication of progress in the prophase stages. Following these three cells are five, 12 to 17, whose nuclei are evidently in the spireme stage. The continuity of the dense, dark bands or ribbons is not shown, of

course, since the photograph does not show the vertical extent of the elements. A comparison of these five nuclei one with another shows little difference in appearance. They are essentially in the same stage.

The change from cells 11 and 12 is not very marked, but between 16 and 17 at the other end of the series the change is striking and abrupt. The chromosomes are apparently fully formed in cells 17 to 20, and are certainly approaching the equatorial plate stage. Cell 21 appears as if it might be a polar view of an equatorial plate in which, of course, some of the chromosomes are slightly out of focus. The nuclei in cells 22 to 27 are plainly in the equatorial plate stage. Cell 27 shows the monaster in oblique or polar view, while cells 22 to 26 show the plate in profile view. Next comes a series of seven anaphases, 28 to 34, so similar in appearance that it is impossible to determine whether any one is further advanced than another. In these cells the chromosomes tend to lie at the ends or in diagonally opposite corners of the cells. One group of the chromosomes in cell 29 is below the plane of focus. In cells 28 and 30 certain of the long chromosomes project upward perpendicularly to the focal plane and appear in end view. The filament as a whole from apex to base shows about six stages in nuclear division, of which the earliest is represented by about ten nuclei, and the remainder by from five to seven each. The transitions between the groups, with the exception of the first and second, are quite marked and abrupt.

In the terminal portion of the filament shown in figure 12 there appears to be a more gradual and perhaps more continuous series of early and late prophase nuclear changes which may be regarded as phases of a wave which reaches its crest in the equatorial plate stages in cell 17. The first nine nuclei show but slight differences in appearance, although in cells 5 and 9 the light and dark nuclear elements are perhaps more sharply differentiated than in cells 1, 2, 3, and 4. In the succeeding cells the dark elements in the nuclei appear to become more dense, larger in size and perhaps smaller in number, so that if cells 1 and 12 are compared a marked change in appearance is obvious. This change becomes more pronounced in cells 13, 14, 15, and 16. The differentiation of the chromatic elements becomes more and more sharp. Up to cell 16 the prophase

changes are fairly gradual and continuous, but with cell 17 a conspicuous jump to polar view of the equatorial plate stage occurs. The remaining twenty cells of this filament which are not included in the figure are polar and other views of the equatorial plate stage of division.

The conspicuous fact as to the seriation of the division stages in this filament is, as noted, that it is discontinuous, or by groups of nuclei. With reference to the question whether we can distinguish certain stages as more persistent while others are more transitory, I have studied a considerable number of filaments and tabulated the data as to the relative number of cases of each stage which are found in such preparations.

In filament 4 we have a discontinuous but successive series of division stages which begins with a polar view of an equatorial plate at the apex and ends with the completion of the wall between the daughter cells at the base. This filament is from an antheridium of *Nitella flexilis*, which has twelve chromosomes of variable sizes. A series of polar, oblique, and profile views of equatorial plate stages begins with the first cell and extends to cell 15. The nuclei in cells 15 to 18 appear to be early anaphase stages, in which the elements are plainly more slender than in cells 1 to 15. These are the chromosomes as they begin to separate. There is then a sharp transition to three late anaphases, cells 19, 20, and 21, in which the chromosomes lie in two sharply differentiated groups more or less diagonally placed in the cells. Next follows a series of diaster stages in the nuclei of cells 22 to 27. The daughter chromosomes are massed and lie pressed closely against the end walls of the mother cells. The equatorial ends of the individual chromosomes are still free and distinct in these cells, but they do not appear as sharp in outline and as optically homogeneous as in the preceding cells. The end of this group or series is not plainly recognizable. The transition to the telophases is very gradual. Perhaps cell 27 begins a series of later stages. In cell 28 the individual chromosomes are all rounded in, to form in edge view two oblong masses still closely pressed against the ends of the mother cells. Nuclear membranes around the daughter nuclei are doubtless present at this stage. In cell 27 the evening up of the surfaces of the daughter groups of chromosomes is in progress.

The period of greatest density of the daughter groups is shown in cells 28 to 30. In cell 31 they are perhaps slightly less homogeneous in appearance and slightly increased in volume. Individual chromosomes are still in some degree recognizable as large and dense elements in the daughter nuclei, showing that they have not yet passed into the resting condition. In cells 32 to 40 we have a very evenly graduated series of stages in the transformation of the chromatic masses into smaller units. In cells 40 to 48 we have perhaps so-called resting nuclei, although the dark elements in the nuclei are still somewhat elongated and irregular, which is suggestive of late telophase.

In cells 29 to 39 we have perhaps successive stages in the development of the cell plate and cell wall. In cell 29 we see a faint indication of a plate in the equator of the cell. This plate becomes more conspicuous in cells 30 to 37 and appears to grow centrifugally outwards. In cells 37 and 38 it appears to extend completely across the mother cell. In cell 39 the wall is apparently completed. With its completion a slight equatorial constriction appears in the outline of the mother cell, indicating the rounding up of the daughter cells. This constriction is first visible in cell 39. This becomes more pronounced, until in cells 47 and 48 the convex outlines of the original mother cells are replaced by those of the two new individual cells, which together are the same size as the mother cell.

A somewhat similar but shorter and more discontinuous series is shown in figure 8, representing a young filament from *Chara delicatula*, a species with more than forty chromosomes. Cells 1 to 5 plainly show profile and polar views of equatorial plate stages. The next three cells are in late anaphase, in which the groups of chromosomes tend to lie diagonally placed in the ends of the cells. Cell 8 is perhaps in very early telophase previous to cell plate formation. In the remaining cells the plate extends completely across the equator of the cell, and we have here perhaps so-called resting nuclei.

These four filaments thus show fairly well graded series of nuclear and cell division stages. However, each successive cell from apex to base is not recognizably in a slightly different stage of division than the preceding one. In this respect the seriation of the division stages is discontinuous, but, none the less, progressive by linear groups in which the different cells in a linear

group show a high degree of synchronism. This is very obvious in filament 4, for instance. As has already been noted, cells 1 to 15, 15 to 19, 19 to 22, 22 to 27, and 39 to 50 constitute distinct linear groups, the cells of each of which show more or less complete synchronism as to the stages which they show.

In this respect the seriation of the division stages in these filaments is similar to that which Soltwedel, Strasburger, and Němec found in the embryo sacs of *Dictamnus*, *Fritillaria*, and certain other Angiosperms, and that reported by Kurssanow in *Vaucheria*. If we examine figure 1, plate 1, of Strasburger (1884a) and Soltwedel's figure 40, plate 17, we find that each succeeding nucleus from the micropylar to the chalazal end of the embryo sac is not in a slightly later stage of division than the

TABLE I.

Showing the number of nuclei in each group of the successive division stages in the embryo sacs of Fritillaria imperialis and Dictamnus albus as given in the figures of Strasburger (1884) and Soltwedel (1882).

PLANT	NO. OF RESTING NUCLEI	NO. OF PRO-PHASES	NO. OF EQUA. PLATES	NO. OF META-PHASES	NO. OF ANA-PHASES	NO. OF EARLY TELO-PHASES	NO. OF LATE TELOPHASES CELL PLATE
Fritillaria	0	10	23	3	8	6	4
Dictamnus	6	8	10	0	11	11	7

preceding one, but that a group of nuclei in practically the same stage is followed by other groups in different successive stages of division. With the view of presenting this more concretely I have tabulated the number of nuclei in each group of the successive division stages in the embryo sacs of *Fritillaria* and *Dictamnus* as given in Strasburger's and Soltwedel's figures (TABLE I). At the bottom of Strasburger's figure is a group of late prophases, perhaps ten, which is followed by another group of about 23 nuclei in the equatorial plate stage. The transition between the two groups is quite marked. Next follows a small group of metaphases (three nuclei). The next group consists of about eight anaphases. Then follow approximately six early and four late telophase stages. The transitions between these stages are fairly abrupt, so that the seriation of division stages throughout the length of the embryo sac is clearly dis-

continuous, but progressive by groups. This discontinuity in the seriation is also conspicuous in Soltwedel's figure, which shows six stages in division, each of which is represented by groups of from 6 to 11 nuclei. The transition between these groups is quite marked and abrupt.

In the seriation of the division stages in *Vaucheria*, Kurssanow (1911) describes but four stages, two of which are grouped together as ana- and telophases. TABLE 2 shows Kurssanow's tabulation of the length in microns of the regions occupied by the successive stages of division in what he calls 'division waves.'

TABLE 2.

Showing the length in microns of the regions occupied by the successive stages of division in 'division waves' in three species of Vaucheria as given by Kurssanow.

PLANT	PRO-PHASE	META-PHASE	PRO-PHASE	ANA- AND TELO-PHASE	AL-READY DIVID-ED NU-CLEI	ANA- AND TELO-PHASE	META-PHASE	PRO-PHASE	LENGTH OF WAVE	NO. OF DIVID-ING NU-CLEI
V. repens	200μ 21%	540μ 58%		200μ 21%					940μ	550
V. terrestris	720μ 27%	1440μ 54%	430μ 19%						2590μ	570
V. terrestris	830μ 27%	560μ 29%		560μ 29%					1590μ	250
V. uncinata	1000μ	2930μ		1920μ	620μ	1170μ	2370μ	2250μ	12210μ	2300

He finds that the transitions between prophase and metaphase, metaphase and anaphase, and anaphase and telophase stages is abrupt, so that the 'wave' can be divided into distinct regions with reference to particular stages. It is to be noted that the metaphase stages are perhaps the most persistent, since they occupy twice the distance in microns of the prophase, anaphase, and telophase stages. This persistency of the metaphase stage is similar to that in the maturation divisions in certain animal eggs. In *Chaetopterus*, *Cerebratulus*, and *Amphioxus*, for instance, this stage persists for a considerable time, indicating perhaps that the metaphase is a condition of relative stability.

That in some cases the stages of division may be almost completely synchronous throughout entire filaments is well illustrated in figures 2 and 6. Figure 2 shows a filament of cells most of which are very similar in appearance and plainly in the telophase stage of division. The first eight cells are apparently earlier telophases than the rest, since no cell plate is visible. In the remaining cells of the filament the plate is more or less completely developed across the equator of the cell, although in cells 10, 11, 20, 29, 32, and 36 it is perhaps least conspicuous. The chromosome groups or daughter nuclei in edge view are more or less oblong, and lie flattened against the end walls of the mother cells. This condition is particularly characteristic of the very late telophases.

Figure 6 shows 28 cells of a long filament, which from apex to base consisted of 84 cells. The equatorial constriction in the outlines of the mother cells indicates that the new cell wall is completely developed, and that in reality the filament consisted of 168 newly formed individual cells similar in size and appearance. The outlines of the mother cells, however, are still to be recognized. There seems to be no difference in appearance in any of the cells throughout the entire filament. The nuclei of the daughter cells are apparently in the resting stage, although in edge view they are still oblong and somewhat flattened. Within the nuclei may be seen large numbers of somewhat elongated, irregular dark elements, which are undoubtedly the result of the breaking up of the telophase chromosome masses into smaller elements. The dark elements in these nuclei, however, do not appear as finely divided as those in the resting nuclei in figure 3.

These two filaments are characteristic of what may frequently be found in an antheridium. It is not uncommon to find long filaments consisting of nearly a hundred cells, all in the late telophase or so-called resting stage. In this respect these filaments are in sharp contrast with such filaments as are shown in figures 4, 8, 12, and 13, in which there is a progressive seriation of the division stages.

The seriation of the division stages may progress either from apex to base or the reverse. A series may begin in the middle of a filament. In such cases the earlier division stages may be found in the middle of a filament with successively older stages

occurring in both directions towards the apex and base. Such cases are similar to those described by Němec in latex tubes, and by Kurssanow in *Vaucheria uncinata*. One may also find division stages indiscrimately intermingled. A telophase stage may be found between two resting cells, and these in turn may be adjacent to metaphase stages, etc.

In filament 1, figure 9, the first three cells at the apex are plainly in late telophase stages, while the remaining cells are in early prophase. Similarly in figure 7, the cells of the apical portion of the central filament show equatorial plate views, while the rest of the cells are in early prophase or perhaps in the resting condition. The fact that the early stages of division are not always to be found in the apical portion and successively later stages toward the base of the filament is further illustrated in figures 3, 7, 11, and 14.

Close proximity of widely different stages is well illustrated in figures 1, 3, 5, 7, 10–12, and 14. In figure 10 the transition is from equatorial plate to telophase; in figure 3 from equatorial plate to resting cells; in figure 14 from telophase to equatorial plate; in figure 11 from early telophase to resting cells; in figure 12 from late prophase to equatorial plate, and in figures 1 and 5 from spireme stages to early telophases. These linear groups of cells are each apparently in almost exactly the same stage of division.

The largest number of cells in the filaments and portions of filaments shown in plate 1 are in early and late telophase stages. The equatorial plate and late anaphase stages come next in numbers. The leptonema stage is not easily recognizable in microphotographs, but the thick spireme is shown by a fairly large number of cells. TABLE 3 shows the grouping of the cells in entire filaments and parts of filaments chosen to photograph because they showed figures of one stage or another of division. In choosing the filaments to photograph there was doubtless selection of the material favoring certain division stages which are more conspicuous in aceto-carmine preparations and appear more sharply differentiated and clear when photographed. The table shows material from 55 filaments and parts of filaments. A more complete tabulation of division stages as found in perhaps less selected filaments is now being made.

This table shows, as also noted in plate 1, that the early

and late telophases are the most numerous and are found in 18.7 and 12.6 percent respectively of the total number of cells.

TABLE 3

FILAMENT NO.	RESTING NUCLEI	EARLY PROPHASE LEPTONEMA	TRANSITION	THICK SPIREME	LATE PROPHASES TRANSITION	EQUATORIAL PLATE	METAPHASE	EARLY ANAPHASE	LATE ANAPHASE	DIASTER	DI-SPIREME	EARLY TELOPHASE	LATE TELOPHASE	TOTAL NO. OF CELLS IN THE FILAMENTS
1	.....	.....	.....	.....	.....	.....	.....	.....	.....	4	5	.....	.....	9
2	.....	.....	.....	.....	.....	4	.....	.....	.....	.....	.....	.....	.....	4
3	.....	.....	.....	8	.....	8	.....	.....	.....	.....	.....	.....	.....	16
4	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	8	.....	.....	8
5	.....	.....	.....	15	.....	.....	.....	.....	.....	.....	.....	4	.....	19
6	.....	.....	.....	12	.....	4	.....	.....	.....	.....	.....	.....	.....	16
7	.....	.....	.....	.....	.....	.....	.....	.....	.....	4	.....	.....	.....	4
8	.....	8	.....	.....	.....	.....	.....	.....	4	1	3	.....	.....	16
9	12	.....	.....	.....	4	4	.....	.....	.....	.....	.....	.....	.....	20
10	.....	8	.....	.....	.....	.....	.....	.....	.....	8	.....	.....	.....	16
11	.....	.....	.....	.....	.....	14	.....	5	3	6	11	.....	12	51
12	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	12	38	.....	50
13	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	84	84
14	.....	.....	.....	.....	.....	4	.....	.....	.....	4	1	12	4	25
15	.....	.....	.....	.....	.....	8	.....	.....	.....	.....	.....	.....	.....	8
16	18	.....	.....	.....	2	6	.....	.....	.....	.....	.....	.....	.....	26
17	50	.....	.....	.....	.....	.....	.....	.....	.....	4	4	.....	.....	58
18	.....	.....	.....	4	.....	.....	.....	.....	.....	12	.....	20	.....	36
19	.....	.....	.....	8	.....	.....	.....	.....	.....	.....	.....	.....	.....	8
20	.....	.....	.....	.....	4	18	.....	.....	.....	.....	.....	38	8	68
21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	15	.....	15
22	.....	.....	.....	.....	10	.....	.....	.....	.....	.....	.....	.....	.....	10
23	20	4	.....	.....	.....	15	.....	.....	18	6	20	.....	.....	83
24	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	10	.....	.....	10
25	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	36	.....	.....	36
26	14	.....	.....	.....	.....	8	.....	.....	.....	.....	.....	20	.....	42
27	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	30	.....	30
28	.....	.....	.....	7	.....	.....	.....	.....	.....	.....	.....	.....	25	32
29	.....	.....	.....	48	.....	.....	.....	.....	.....	.....	.....	.....	8	56
30	.....	14	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	14
31	.....	.....	.....	4	10	.....	.....	.....	.....	.....	.....	.....	.....	14
32	.....	.....	.....	8	22	.....	.....	.....	.....	8	6	.....	.....	44
33	.....	.....	.....	8	.....	.....	.....	.....	.....	.....	.....	.....	.....	8
34	.....	.....	.....	.....	15	.....	.....	.....	.....	8	.....	.....	.....	23
35	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	8	8
36	.....	.....	.....	.....	.....	.....	16	.....	.....	.....	.....	.....	20	36
37	32	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	32
38	.....	.....	.....	.....	.....	.....	12	.....	.....	.....	.....	.....	.....	12
39	.....	20	.....	.....	.....	32	.....	.....	.....	.....	8	.....	.....	60
40	.....	.....	.....	.....	.....	.....	.....	.....	.....	8	7	.....	.....	15
41	.....	.....	.....	.....	8	.....	.....	.....	.....	.....	.....	.....	.....	8
42	.....	20	.....	.....	.....	.....	.....	.....	.....	.....	.....	9	6	35
43	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	8	15	.....	23
44	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	8	.....	8
45	.....	.....	.....	4	.....	.....	.....	.....	.....	.....	.....	8	.....	12
46	.....	.....	.....	4	.....	.....	.....	.....	.....	.....	.....	.....	.....	4
47	.....	.....	.....	.....	8	.....	.....	.....	.....	.....	.....	.....	.....	8
48	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	15	.....	.....	15
49	.....	8	.....	17	.....	.....	.....	.....	.....	.....	.....	.....	.....	25
50	.....	.....	.....	.....	.....	16	.....	.....	.....	12	.....	.....	.....	28
51	.....	.....	.....	.....	.....	.....	.....	.....	11	.....	.....	.....	.....	11
52	.....	.....	.....	.....	.....	8	.....	.....	.....	4	.....	.....	.....	12
53	.....	.....	.....	.....	.....	7	.....	.....	.....	.....	.....	42	.....	49
54	.....	.....	.....	12	8	.....	.....	.....	.....	.....	.....	.....	.....	20
55	.....	.....	.....	5	.....	.....	.....	.....	.....	.....	.....	.....	.....	5
Totals	146	82	0	164	91	156	28	5	36	89	154	259	175	1385
Percent.	10.5	5.9	0	11.8	6.5	11.2	2.02	.36	2.5	6.4	11.1	18.7	12.6	

Spireme stages, resting nuclei, equatorial plate, and dispireme stages come next in frequency in the order named. No transition stages from early prophase and leptonema to thick spiremes were recognized. Similarly the number of metaphase and early anaphase stages is very small. However, the group of filaments given in this table is undoubtedly a selected one, and since early prophases, metaphases, and early anaphases are perhaps less clear in aceto-carmine preparations, and more difficult to show clearly in microphotographs than some other stages, there was perhaps some elimination of filaments in which these stages were most abundant.

The great frequency of early and late telophase stages shown in this table is very much in contrast with the data given by Kurssanow from *Vaucheria*. Kurssanow reports, as is shown in table 2, that in all cases with the exception of one the metaphase stages occupied more than fifty percent of the length of the 'division wave.' However, since he does not tabulate the number of nuclei in each stage of division, it is impossible to make direct comparison with the data from my tabulation. Assuming that the nuclei are more or less evenly distributed in the *Vaucheria* filaments, we can calculate, from the percentages given and the total number of dividing nuclei in Kurssanow's table, the approximate number of nuclei in each stage of division. In the 570 dividing nuclei in *V. terrestris*, for instance, we would thus have 151 nuclei in the prophase stages, 307 in the metaphase, and 108 in the ana- and telophase stages. The comparatively small number of anaphase and telophase stages here is quite in contrast, as noted, with the great frequency of such stages in my tabulation of the division stages in the antheridial filaments of the Characeae.

DISCUSSION

It is perhaps premature to attempt to analyze any of the appearances in these nuclear figures in terms of colloidal behavior. The changes from late anaphase to the resting condition do, however, suggest the possibility of such an analysis. As they reach the poles the chromosomes appear less dense and less homogeneous optically, and within each chromosome appear light areas or elements. What these light elements are is not obvious from the photographs. They may be more watery

areas or phases in the chromosomes, or possibly regions where the chromatic substance is less dense.

In the gradual transition from anaphase to telophase, cells 26 to 29 of filament 4, perhaps, the individual chromosomes become rounded in, and the surfaces of the daughter groups begin to even up. The individual chromosomes, however, are still recognizable to some degree as large and dense elements in the daughter nuclei. The mass as a whole is, however, very dense. The daughter nuclei are perhaps darkest and densest in cells 28 to 32, but they are still optically heterogeneous, with numerous light areas, 'alveoles' or elements. Beginning with cell 32 the daughter nuclei appear to increase somewhat in size, and this is apparently accompanied by an increase in optical heterogeneity. The dark elements seem to break up into smaller irregular units, and the light elements appear to become more numerous and perhaps sharper. This breaking up of the denser elements continues until in the nuclei of cells 39 to 48 they appear as irregular, apparently connected, but more or less evenly distributed particles. However, there is nothing in the photographs to suggest that the dense particles are rounded and distinctly separate. They are plainly irregular in outline and appear to be more or less connected. The outlines of the light areas or elements likewise appear irregular. They perhaps constitute a continuum in which the denser elements are imbedded.

A close examination of the mass changes that have occurred in the nuclei of cells 19 to 48 suggests a breaking up of the chromosomes into smaller and smaller elements as the reconstruction stages progress. The colloidal changes involved in this transformation are by no means clear, but may perhaps be analogous to an increase in degree of dispersion of the particles of the discrete phase of colloids *in vitro*. The emergence of light areas or elements in the anaphase and early telophase chromosomes gives the nuclei somewhat more of the optical appearance of two phase systems. Each chromosome appears as a two phase system suspended or dispersed in the enchylematic continuum. In the diaster stages in cells 22 to 27 the light elements appear to constitute the disperse phase in the denser, more chromatic continuum. As noted before, they apparently constitute more watery and less chromatic material in the chromosomes. At

the end of the anaphases the chromosome groups appear quite solidly chromatic.

In the changes from anaphase to telophase in cells 27 to 40 the boundaries of the chromosomes become less sharp, and their material becomes more diffuse. The lighter elements appear to become continuous, thus causing perhaps the dispersed appearance of the chromosomes as the telophases advance. If this is what actually occurs, the light elements then come to make up the continuous phase, with the denser elements imbedded in it. We would thus have an interchange in the relations of the elements which resembles phase reversal. However, it is to be noted that the dense elements in the nuclei of cells 39 to 48 are not rounded up into separate particles or droplets, such as one would expect to find in the disperse phase of an oil-in-water emulsion, for instance, but that they appear to be continuous with another. Moreover, it is not certain, but perhaps possible, that the light and less dense areas or elements, the nuclear enchylema, in these nuclei have been derived or made up largely of such light elements as appeared at first in the dispireme and early telophase chromosomes of cells 26 to 30. This continuum of enchylema obviously increases in volume. It is not impossible that the lighter continuum in the late telophase nuclei may in part have another origin, perhaps from the cytoplasm. There is nothing, however, in the photographs to differentiate a so-called achromatic chromosomal material from the karyolymph or from invading cell sap. Optically, the light elements in the diaster and late anaphase chromosomes and late telophase nuclei have the same appearance.

Whether or not anything analogous to phase reversal is involved in these late anaphase changes and telophasic reconstruction of daughter nuclei is of course not as yet clear. As noted, the photographs indicate that when the chromosomes reach the pole they form a very densely compacted mass. Whether there are no interspaces with watery inclusions is not readily determinable. The conditions in fixed and sectioned material, with the possibility of shrinkage involved in such methods of preparation, are not to be regarded as at all conclusive on this point. As to the method by which the chromosomes return to the more diffuse condition of the resting nucleus, two general view-points are strongly represented in the literature.

Gregoire and his school hold that during the reconstruction of the daughter nuclei numerous vacuoles develop within the chromosomes, which enlarge, run together, and finally break through the chromosomal boundaries, so as to produce the internal reticulated and net-like structure of the resting nucleus. Boveri and his school, on the other hand, maintain that the daughter chromosomes change or pass over into a network or reticulated structure by sending forth branches or pseudopodia which anastomose. In the interspaces of these anastomosing branches is held part of the enchylema. The final results of either the vacuolizing or the anastomosing process would be much the same in optical appearance.

It seems fairly clear that the late telophase chromosomes are in transition from the form they have maintained by virtue of their viscosity as semi-liquid or solid gels to the more plastic and perhaps more liquid condition of the resting nucleus.

The current view, that the telophases involve the breaking up of the chromosomes into smaller and smaller units, and a more or less even distribution of the chromatic elements, is perhaps analogous to the phenomena of increase in degree of dispersion of the discontinuous phase in colloids *in vitro*. The changes in the chromosomes as the late telophases progress might then be considered as a continued increase in degree of dispersion of the chromatic elements until a state like that of the resting nucleus is reached. Ostwald (1909, 1917) finds that as gels take up water and swell an increase in degree of dispersion occurs, and Gaidukov (1910) reports that with this increase in degree of dispersion the ultramicroscopic gel particles lose their highly refractive character. It is well known from the study of both fixed and living material, and is well illustrated in cells 39 to 48 in filament 4, that the telophase nuclei are of greater volume than the late anaphase groups of chromosomes. This is generally regarded by cytologists as associated with the dissolution of the chromosomes. The loss of refractive character of the gel particles which accompanies increase in degree of dispersion, according to Gaidukov, is in line with the observations of Della Valle (1913) Rhumbler (1914) Chambers (1924) Lewis and Lewis (1924) Schaede (1925, 1926) and my own (1926) that the living resting nucleus, the stage in which the degree of dispersion of the chromatic elements is perhaps highest, is

optically relatively homogeneous and shows little or no structural differentiation. In the prophases, metaphase and early anaphase, on the other hand, the chromatic elements or chromosomes are sharply differentiated. Optical homogeneity, however, is not always an indication of a high degree of dispersion, since many gels whose degree of dispersion is very low appear optically homogeneous.

So far there is nothing known as to the behavior of colloids *in vitro* which would justify the interpretation of chromosomal alveolization as a process of equational splitting or the division of the chromatic elements into parallel daughter strands.

We may now turn to a consideration of the prophase changes in the nucleus. I regard the nuclei in the end of filament 3 as fairly typical of resting nuclei stained with aceto-carmine. Optically these nuclei consist of light and dark elements, and in general somewhat resemble two phase systems. The dark elements are plainly irregular in contour, somewhat elongated and apparently more or less connected. There is some suggestion that the structure is a reticulum of dense dark elements more or less connected by paler and thinner elements. The first eight nuclei of filament number 13 appear to be very early prophases, and there is little difference in appearance between any of these nuclei. However, if these nuclei are compared with those just described in filament 3 a marked difference in appearance can be recognized. The nuclei in cells 9 and 10 are quite different from the nucleus in cell number 8 in that the dark elements appear larger, perhaps denser, more sharply outlined, and apparently fewer in number. Nucleus number 11 shows the dark elements still more sharply differentiated. The light areas or elements likewise appear more continuous and of increased total area. The evidence that they perhaps constitute a continuous phase, in which the dark elements are dispersed, is apparently more convincing.

The prophase changes up to this point appear optically to consist in a decrease in the degree of dispersion of the dense elements, which thus become larger, irregular and more definitely connected bodies. The gradual transformation of these dense chromatic particles into long bands or ribbons to form the spireme is not well shown in this filament. Such a change is not paralleled by any known change of colloids *in vitro*. Decrease

in degree of dispersion or the collection or condensation of dispersed particles into larger units in an unorganized colloid does not result in the formation of homogeneous strands or bands of constant diameter and number. On the other hand, a certain parallelism is suggested between these prophase changes and the transformation of a sol into a more or less stranded gel. The prophase changes are essentially condensation processes. In the gelation of certain colloids such as gelatin, agar, albumin, starch, etc., as has been shown by Bachman (1912) Ostwald (1909, 1917) Zsigmondy (1920) Laing and McBain (1920) and Holmes (1923), a decrease in degree of dispersion and an increase in the size of the particles occurs. The size that the dispersed particles will have depends to a considerable degree on the conditions under which the gelation occurs. In a gelatin-water-alcohol system, Hardy found that the droplets constituting the disperse phase were excessively minute if the mixture was cooled rapidly, but if the cooling was slow the droplets were often as much as 10 microns in diameter. Ostwald reports that an increase in viscosity generally accompanies a decrease in the degree of dispersion. Such an increase in viscosity accompanying a decrease in degree of dispersion is in line with the observations of Chambers, Heilbrunn, Ödquist, and Zimmerman (1923), that the viscosity of protoplasm is highest during mitosis, a period in the life of the cell in which the degree of dispersion of the chromatic elements is generally regarded as being lower than during the so-called resting stage. The appearance of the late prophase, equatorial plate, metaphase and early anaphase chromosomes is certainly suggestive of a semi-liquid or solid gel. This appearance of a gel- or semi-solid-like consistency has been confirmed by the microdissection studies of Chambers and Sands (1923) and Chambers (1924) in which they found that the chromosomes in these stages are highly viscous and very elastic.

It is to be particularly noted in the filaments shown in plate 1, and as has been shown by Chambers (1924) Lewis and Lewis (1924) and Schaede (1925) that the region of the spindle is optically homogeneous. In none of the cells here shown are spindle fibers visible, and there is nothing in this region to suggest a two phase colloidal system, such as 'kinoplasm' and 'trophoplasm.' However, when the cell plate begins to develop,

as is shown in cells 31 to 39 in filament 4, it appears as a highly refractive line or band in the equator of the cell.

It is to be noted that synchronism in nuclear division is very general in multinucleated cells associated with reproduction. The nuclei in coenocytic sporangia, antheridia, oogonia, asci, basidia, embryo sacs, endosperm, and in fertilized eggs of many animals generally divide simultaneously. This is quite in contrast with the more or less independent division of the nuclei in meristematic vegetative cells and tissues, although in latex tubes, primordia of vascular elements, and in filaments of *Vaucheria* the nuclei show some degree of synchronism in division. This synchronism in nuclear division in reproductive cells may perhaps be associated with the fact that the nuclei in such structures are largely of the same or nearly the same age. This is without doubt true of the nuclei in basidia in which we find conjugate nuclear division. Whether or not the nuclear divisions are completely synchronous appears to be associated in some degree with the size of the coenocytic unit and with the number of nuclei. In comparatively small structures such as antheridia, oogonia, asci and basidia the nuclei, as noted, are generally to be found at any one time in the same stage of division throughout the entire cell, and the synchronism is thus complete; while in large coenocytes such as embryo sacs, sporangia, etc., the synchronism as to the particular phases of division is less complete. The various stages of division may be found to form a more or less progressive series of successive stages.

The seriation of the division stages in such cases, however, is discontinuous in the same manner as I have described it for the antheridial filaments of the Characeae shown in plate 1. Each successive nucleus is not recognizably in a slightly later stage of division than the preceding one, but a group of nuclei in practically the same stage of division is followed by other groups in different successive stages of division.

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Explanation of plate 1

All photographs are of aceto-carmine preparations of antheridial filaments taken from fifteen minutes to two hours after mounting with a Zeiss 6 mm. and a 2 mm. apochromatic objective n.a. 1.30 and compensating oculars 6 and 8. The approximate magnifications are given with each figure.

FIG. 1. A portion of a young filament of *Nitella flexilis* showing an abrupt transition from spireme to telophase stage of division. × 1000.

FIG. 2. A filament of *N. flexilis* consisting of thirty-eight cells in early and late telophase stages of division. × 1000.

FIG. 3. A portion of a filament of *N. flexilis* showing an abrupt transition from equatorial plate stage of division to resting cells. × 1000.

FIG. 4. A filament of *N. flexilis* showing a progressive but discontinuous series of division stages from equatorial plate at the apex to resting cells or perhaps late telophases at the base. × 1000.

FIG. 5. A portion of a short filament of *N. flexilis* showing an abrupt transition from spireme stage to late anaphase or perhaps early telophase stage of division. × 1000.

FIG. 6. A short portion of a long filament of *N. flexilis* showing twenty-eight cells in the very late telophase stage of division or perhaps in the resting condition. The synchronism in division in this filament is complete. ×1000.

FIG. 7. Three young filaments of *N. flexilis*. × 200.

FIG. 8. A young filament of *Chara delicatula* showing a progressive but discontinuous series of division stages from polar view of equatorial plate to late telophase or perhaps resting cells. × 400.

FIG. 9. A group of young filaments of *N. flexilis* showing various stages of division. × 200.

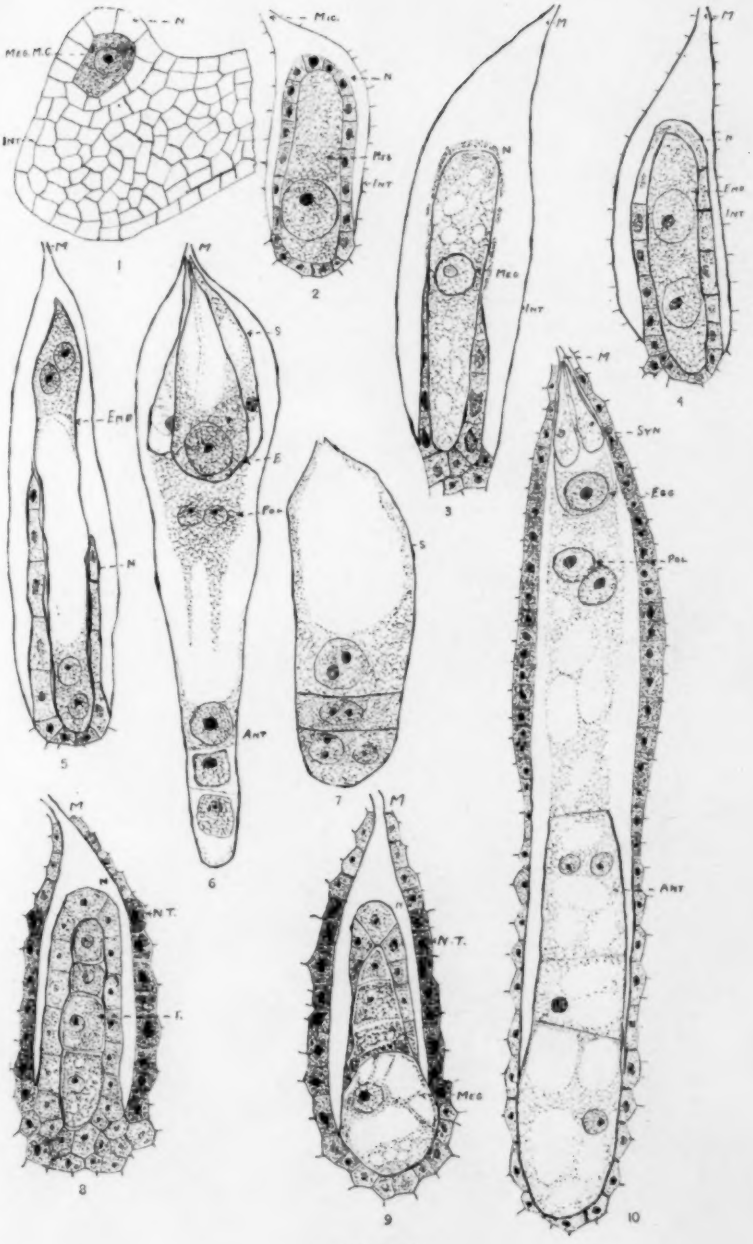
FIG. 10. A portion of a filament of *N. flexilis* showing an abrupt transition from equatorial plate stage to telophase. × 1000.

FIG. 11. The terminal portion of a long filament of *N. flexilis* showing an abrupt transition from telophase stage of division to resting cells. × 900.

FIG. 12. A portion of a filament of *N. flexilis* showing a more or less gradual and progressive seriation of early prophase stages of division. ×1000.

FIG. 13. A filament of *Chara coronata* showing a progressive but discontinuous series of nuclear division stages beginning with early prophase at the apex and ending with anaphases at the base. × 900.

FIG. 14. A portion of a filament of *N. flexilis* showing a transition from late telophase to equatorial plate. × 1000.



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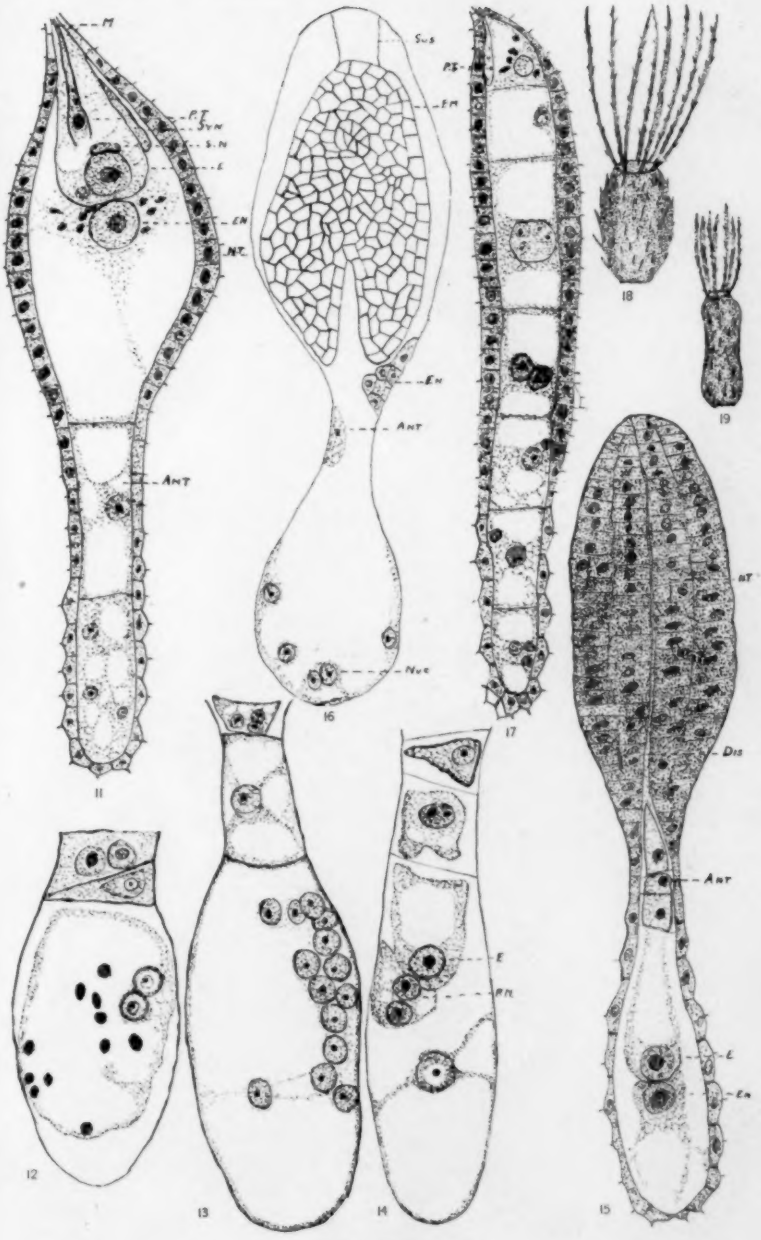

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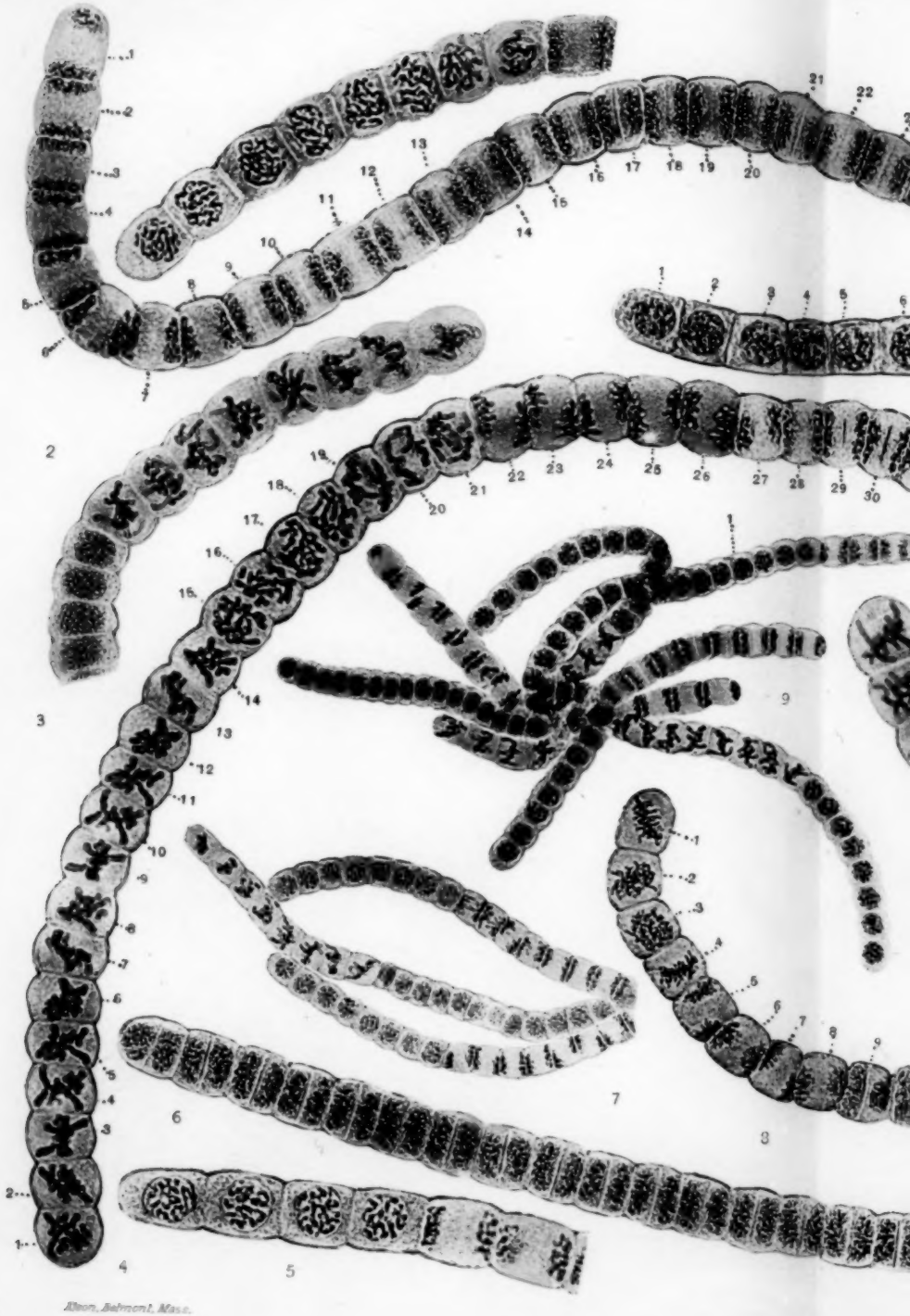

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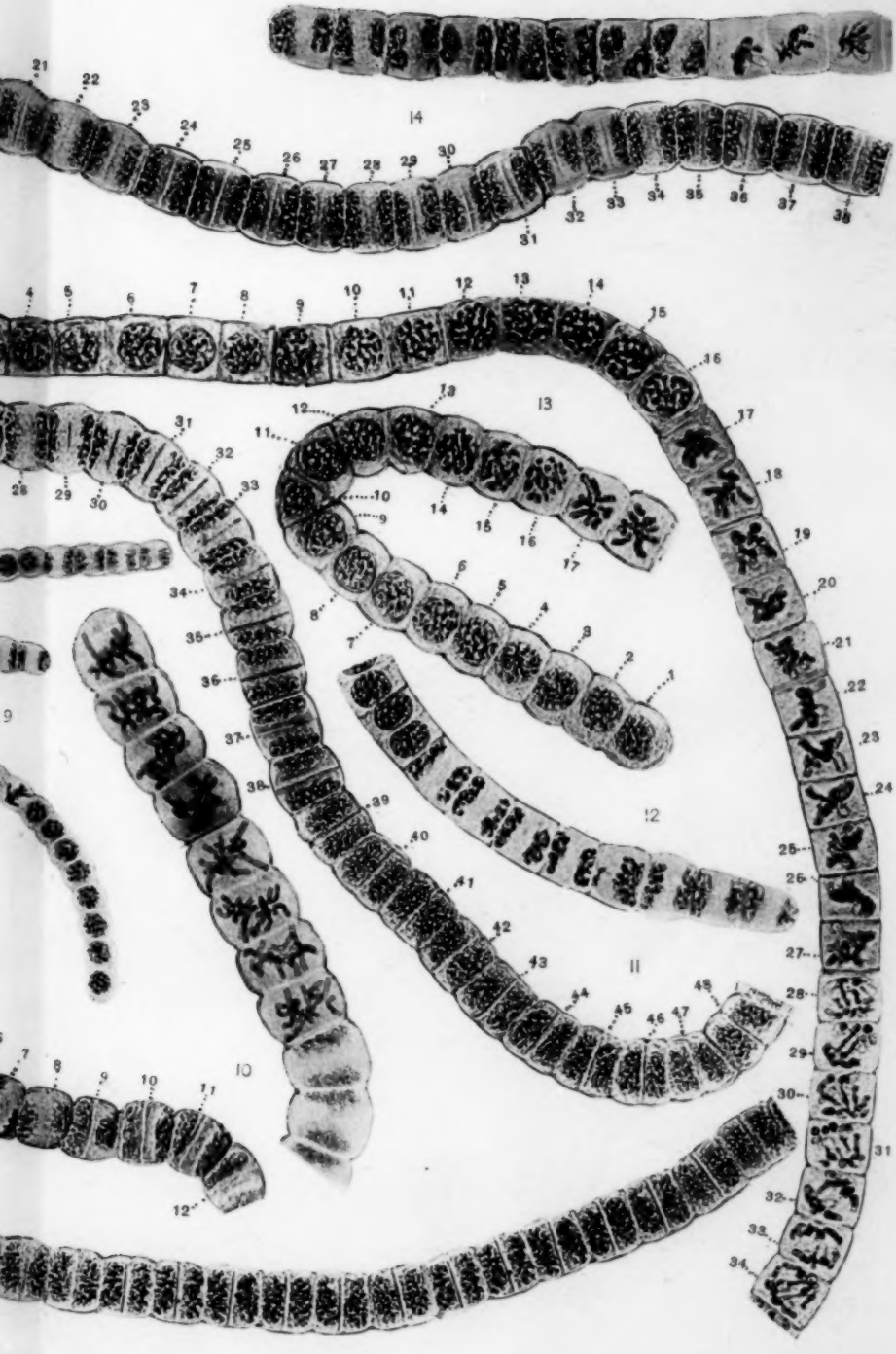
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Susceptibility of wheat to mildew as influenced by salt nutrition

SAM F. TRELEASE AND HELEN M. TRELEASE

(WITH FOUR TEXT FIGURES AND PLATES 2, 3)

In studies of the conditional control of plant disease, it has become increasingly evident that environmental conditions, of temperature, moisture, light, mineral nutrient supply, etc., may have an important influence on the nature and severity of parasitic disease, by modifying the susceptibility of the host, the pathogenicity of the parasite, or both of these complexes of conditions. Thus, information concerning environmental effects in many cases may be as important as knowledge regarding the inherited characteristics of host and of parasite. The present paper relates to the influence of mineral supply upon susceptibility of the host to parasitic disease. It has often been suggested that relatively large supplies of certain compounds of nitrogen in the solution or soil surrounding the roots tend to render plants more susceptible to diseases in general or to certain diseases in particular. Large supplies of phosphates and potassium salts, on the other hand, have been supposed in many cases to make the plants less susceptible. The number of detailed studies on this subject has been relatively small, however, and the results are generally difficult to interpret, owing to the extreme complexity of the influential conditions.

Spinks (1913) reported observations on the amount of mildew (*Erysiphe graminis*) that developed on wheat and barley plants supplied with a number of different concentrations and proportions of mineral salts in solution and soil cultures. The plants were heavily inoculated with spores of mildew. Marks were given to each culture in proportion to the amount of mildew present, cultures with only a trace of mildew being marked 1 and those which were most severely attacked being marked 10. Similar tests were made with yellow rust (*Puccinia glumarum*) on wheat. These experiments led Spinks to conclude that susceptibility to mildew and yellow rust in wheat, and to mildew in barley, was increased by providing the plants with large amounts of available nitrogen; ammonium sulphate and sodium

nitrate seemed to be equally effective in this direction. Certain mineral fertilizers, especially phosphates and potassium salts, on the contrary, are reported to have decreased the susceptibility to these diseases, but they did not counteract the effect of large quantities of nitrogenous fertilizers. Lower susceptibility did not appear to be due to lack of food material available for the fungus in the host, because the plants rendered less susceptible by supplying them with larger quantities of phosphates or potassium salts seemed to be as healthy and well-grown as those receiving no such additions.

In connection with a study of the effect of culture solutions on the ratio of top growth to root growth, Turner (1922) observed that the development of mildew on cultures of barley seemed to be directly related to the nitrate concentrations of the solutions that he used. Although he does not give quantitative data on susceptibility, he states that high-nitrate cultures were particularly susceptible to this fungus and could be readily picked out from the others by this fact; medium-nitrate cultures were not so badly affected, and the low-nitrate cultures scarcely at all.

Many investigators have reported that heavy applications of nitrogenous fertilizers tend to increase the severity of rust attacks on wheat. In most cases it is impossible to determine conclusively from the evidence secured whether greater severity of the disease is due to greater susceptibility of the plants or to greater pathogenicity of the parasite (*e.g.*, a larger number of spores per unit area of the host). However, the more severe development of the disease has generally been ascribed, in part at least, to a higher degree of susceptibility of the host. Little (1883), Bolley (1889), Freeman and Johnson (1911), Biffin (1912), Spinks (1913), Hursh (1924), and others have reported that an increased development of rust resulted from heavy applications of nitrogenous fertilizers. Russell (1921) states that an abundance of nitrogen for wheat leads to the development of large dark green leaves which are often crinkled, and usually soft, sappy, and liable to insect and fungous pests (apparently because of the thinning of the walls and some change in the composition of the sap) and to retarded ripening.

Armstrong (1922) noted that conditions were favorable for a heavy epidemic of yellow rust of wheat when a large quantity

of available nitrogen and an abundance of moisture were simultaneously supplied to the plants. Renewed growth was stimulated, the maturation of the plants was considerably delayed, and the cultures assumed the very dark green color characteristic of plants receiving an excess of nitrogen. These conditions in some way afforded a greater opportunity for rust attack, for it was during this period of delayed maturation that the great epidemic of the season developed. Armstrong emphasizes the view that immunity depends not only upon an inherited factor for resistance, but also upon a properly balanced condition of the plant's metabolism.

Heavy applications of potassium salts have been regarded as tending to lower the susceptibility of wheat to rusts (Spinks, 1913). Russell (1921) reports that at the Rothamsted Station potash-starved wheat and mangolds are liable to be attacked by disease, especially where there is an excess of nitrogen, while plants on plots well supplied with potash, though equally liable to infection, remain healthy. He states that flax growers have found that potassium fertilizers increase resistance to attacks of the wilt organism, and that at the Cheshunt Experimental Station liberal treatment with potassium fertilizers makes the tomato plant more resistant to the bacterial stripe disease. Russell adds that potassium fertilizers often afford the simplest method of dealing with fungus diseases and that they are usually more effective than other fertilizers under glass. Very large supplies of phosphates have been supposed to render wheat less susceptible to rusts (Spinks, 1913) or, as a result of hastening maturation, less subject to attack by rusts (Little, 1883; Bolley, 1889; Freeman and Johnson, 1911).

Gassner (1916) reported that, under certain conditions, larger supplies of nitrogenous fertilizers may tend to increase the attacks of rust, and larger supplies of phosphates may tend to diminish them. The action, however, is indirect and depends upon the general complex of internal and environmental conditions.

Stakman and Aamodt (1924) reported the results of extensive experiments and observations, covering a period of eight years, that were made to determine the effect of fertilizers on the amount of stem rust developed on wheat growing on several types of soil. They observed that plants growing in plats

heavily fertilized with nitrogenous manures sometimes were more heavily attacked by rust than those in other plats. They conclude that the heavier attack of rust in these cases was not due to greater susceptibility of the plants; it was considered to be an indirect effect of an increased density of stand and of delayed maturity, which made conditions for infection more favorable and lengthened the time during which the plants could become infected.

The study reported in the present paper was planned in order to obtain some further information concerning the effect that the salt nutrition of the host might have upon the susceptibility of the host to disease. Wheat mildew was chosen as representing a disease which could easily be studied under greenhouse conditions. The specific objects of the work were to determine: (1) whether evidence could be obtained that the susceptibility of wheat to mildew may be significantly influenced by the composition of the culture solution supplied to the roots; (2) whether a culture solution that allows approximately optimum growth of uninfected plants will also allow approximately optimum growth of infected plants; and (3) whether susceptibility to mildew is correlated with the vegetative vigor of the host.

Cultures of wheat were grown in a series of different salt solutions, and the plants were inoculated as uniformly as feasible with the spores of mildew (*Erysiphe graminis*). Notes were made on the appearance of the plants, especially on the development of mildew per unit area of the leaves. After 31 days of growth, the dry yields of the infected plants in the various salt solutions were determined; and these yields were compared with the yields of uninfected plants grown in a similar series of solutions. These observations and comparisons furnished data for a study of the way in which the susceptibility of the host might be influenced by the salt solution supplied to the roots.

The experiments here reported are preliminary in nature. The series of cultures of infected plants is more extensive than that of the uninfected plants, and it was not feasible to grow the two series simultaneously, under exactly the same environmental conditions. The conclusions that may be drawn from the comparisons of these series are necessarily tentative, and further study may modify them in important respects.

METHODS AND EXPERIMENTS

Cultures infected with mildew. The general culture methods employed in this study were essentially the same as those described in previous papers (Trelease and Livingston, 1924; Trelease and Trelease, 1924). Three hundred cubic centimeters of Marquis spring wheat (supplied by Julius Schendel, of Campbell, Minn.) were soaked for three hours in tap water and then germinated on wet filter paper in eight glass culture dishes (24 cm. in diameter). When the primary root of each seedling was about 6 mm. long, selected seedlings were placed upon paraffined bobbinet stretched over each of four enamelled iron pans (25 cm. in diameter and 8 cm. deep) filled with tap water. Each of the pans was placed in a similar, but slightly larger pan, and tap water was poured into the space between the two pans until the level of the water was even with the top of the smaller pan. During the first two days a moist chamber was provided for the seedlings by placing the cover of a glass culture dish on each netting. On the next day, selected seedlings (measuring between 3.5 and 4.5 cm.) were transferred to the culture solutions.

The culture vessels were cylindrical, glazed earthenware jars obtained from the General Ceramics Company. These jars had been baked by a process that rendered them nearly non-porous. Each jar had a capacity of about 7000 cc. and was about 20 cm. in diameter and 23 cm. deep (inside dimensions), the wall and base being about 1.2 cm. thick. For use as a culture vessel, the jar was nearly filled with solution and covered with a paraffined Portland cement disk having five circular openings, in which were set the cork stoppers supporting the plants (plates 2 and 3). Each stopper bore five seedlings, thus making twenty-five seedlings in each culture. Rotating tables were not available, but the cultures were placed on a greenhouse bench where all of the plants were exposed to approximately the same fluctuations in environmental conditions throughout the culture period.

Twenty-nine different culture solutions were employed. Each had a total concentration of 0.02 gram-molecule per liter; the corresponding osmotic values of the various solutions ranged from about 0.7 to about 1.3 atmospheres. The volume-molecular proportions of the three main salts (KH_2PO_4, $Ca(NO_3)_2$, $MgSO_4$) are given in table 1. The compositions of the solutions are represented graphically by means of points shown on the equi-

lateral triangle of figure 1, and near the points are numbers corresponding to the solution numbers in table 1.[1] It will be seen that solution 17 had equal molecular proportions of the three main salts and that the other sets of salt proportions were selected to give very wide ranges of variation from this equality. In addition to the three main salts, each solution contained 0.00001 M $FeSO_4$. The solutions were renewed every five days, each plant being thus supplied with an amount of solution corresponding to about 56 cc. per day.

After the plants had been in the culture solutions for three days, they were sprayed with distilled water, by means of an atomizer, and then inoculated with mildew spores shaken from heavily infected plants. To insure heavy inoculation and to have this approximately the same for all of the plants, a new lot of about twenty-five similarly infected plants was shaken over each culture. Although this method is not entirely satisfactory, it probably gives nearly the maximum possible degree of inoculation per unit leaf area of the host.

The seedlings were grown in the culture solutions for 31 days (February 14 to March 17, 1927), the period after inoculation being 28 days. Then the tops of the twenty-five individual plants of each culture were harvested separately and dried for 20 hours, to an approximately constant weight, at 101° C. The top dry weight of each plant was then determined. The manipulation of the plants probably served to remove many of the fungous spores, but it was impossible to determine the weight of the fungus adhering to and penetrating the leaves. This amount, however, appeared to be small. The means of the yield values, with their probable errors, are given in table 1. The relative yields, given in the last column of table 1, show the means expressed as percentages of the corresponding mean for culture 29. Plates 2 and 3 show the appearance of certain selected cultures immediately before the plants were harvested.

[1] The base of the triangle would represent solutions in which the percentage of KH_2PO_4 molecules is zero, and the upper apex would represent a solution in which 100 percent of the dissolved molecules are KH_2PO_4. Similarly, the left side would represent solutions containing no $Ca(NO_3)_2$, and the right apex would denote a solution in which 100 percent of the solute molecules are $Ca(NO_3)_2$. Likewise, the right side would denote zero percent $MgSO_4$ and the left apex 100 percent $MgSO_4$. Since every solution actually employed in these tests contained all three salts, the points representing these solutions lie in the interior of the triangle.

Cultures not infected with mildew. The cultures which were not infected with mildew were grown from February 6 to March

TABLE I

Salt proportions of culture solutions and mean dry weights of tops of wheat plants infected with mildew (Erysiphe graminis); culture period 31 days (Feb. 14 to March 17, 1927)

SOLUTION NUMBER	MOLECULAR PROPORTIONS*			MEAN DRY WEIGHT OF TOPS	
	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	Actual	Relative
				milligrams	
1	2	2	96	36.0±0.7	48
2	2	18	80	36.8±0.6	49
3	2	49	49	34.3±0.5	46
4	2	80	18	32.9±0.7	44
5	2	96	2	34.2±0.7	46
6	5	5	90	39.9±1.1	53
7	5	15	80	41.0±0.8	55
8	5	47.5	47.5	38.4±0.8	51
9	5	80	15	37.5±0.8	50
10	5	90	5	34.2±0.8	46
11	15	5	80	40.0±1.1	53
12	15	15	70	35.3±0.8	47
13	15	70	15	40.5±0.9	54
14	15	80	5	39.3±0.6	53
15	18	2	80	45.4±0.7	61
16	18	80	2	37.3±1.0	50
17	33.3	33.3	33.3	46.4±0.9	62
18	47.5	5	47.5	45.8±0.9	61
19	47.5	47.5	5	36.7±0.7	49
20	49	2	49	43.6±1.0	58
21	49	49	2	40.8±0.9	55
22	50	18	32	55.4±1.2	74
23	70	15	15	53.3±1.2	71
24	80	2	18	55.3±1.8	74
25	80	5	15	49.0±1.0	66
26	80	15	5	45.9±0.9	61
27	80	18	2	48.7±0.9	65
28	90	5	5	63.2±1.5	85
29	96	2	2	74.8±1.4	100

* The molecular proportions represent percentages of 0.02 gram-molecule per liter. Thus, solution 29 contains per liter: 0.0192 gram-molecule of KH_2PO_4, 0.004 gram-molecule of $Ca(NO_3)_2$, and 0.004 gram-molecule of $MgSO_4$. Also, every solution contains 0.00001 gram-molecule of $FeSO_4$ per liter.

6, 1923, at the Johns Hopkins University, Baltimore. A description of these tests was given in a previous paper (Trelease and Livingston, 1924), and the results are presented here in table 2. Although the complex of influential conditions (aside from mildew infection) was undoubtedly somewhat different for the two sets of experiments, nevertheless the general similarity of the tests appears to allow tentative conclusions to be drawn from a

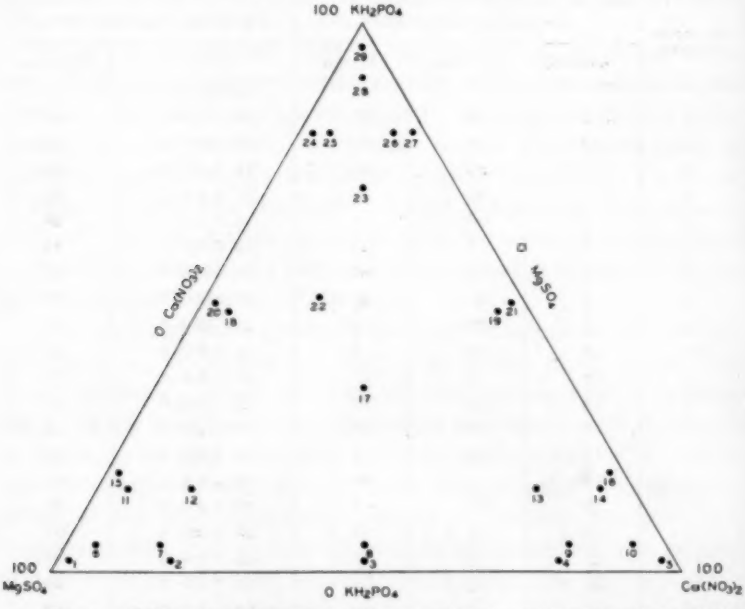

Fig. 1. Culture numbers and volume-molecular salt proportions of the twenty-nine culture solutions. Data are from table 1.

comparison of the results of these two tests. Such a comparison has furnished interesting suggestions, which, it is hoped, may be tested by further experimentation under conditions that are as nearly uniform as possible.

RESULTS AND DISCUSSION

Yields of infected plants

To bring out relations between dry yields of the infected plants and the molecular proportions of the salts employed, the

relative yield values are shown on the triangular diagram of figure 2, which is similar to figure 1 except that the yield values replace the culture numbers, and dots, triangles, and squares are used to represent low, medium, and high yields, respectively. Yields which lie in the lowest quarter of the total range of yields are designated as low, those which lie in the middle one-half of the range are designated as medium, and those which lie in the highest quarter are designated as high.

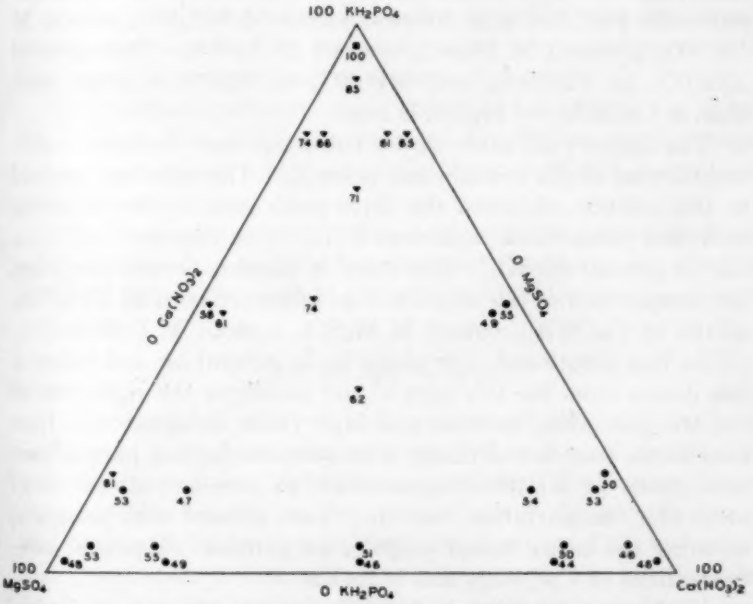

Fig. 2. Relative dry yields of wheat plants infected with mildew. Low, medium, and high relative yields are indicated by dots, triangles, and squares, respectively. Data are from table 1.

A high yield is indicated for only one culture (no. 29), near the upper apex. If a line were drawn from the left apex of the triangle to the middle of the right edge, the low yields would lie on this line or below it, while medium and high yields would lie above it. Only two exceptions are to be noted: culture 11 lying a little above the line has a low yield, and culture 17 situated on the line has a medium yield. Solutions lying below this line are characterized by values of the ratio of KH_2PO_4 to

$Ca(NO_3)_2$ below unity, those on the line have a value of unity for this ratio, while those above the line have values higher than unity.

Culture 29 (see plate 2), giving the highest yield, was supplied with a solution having the following molecular proportions of the three main salts: 96 percent KH_2PO_4, 2 percent $Ca(NO_3)_2$, and 2 percent $MgSO_4$. This solution has the highest tested proportion of KH_2PO_4 and the lowest proportions of $Ca(NO_3)_2$ and $MgSO_4$. The composition of this solution, in gram-molecules per liter, is as follows: 0.0192 M KH_2PO_4, 0.0004 M $Ca(NO_3)_2$, 0.0004 M $MgSO_4$, 0.00001 M $FeSO_4$. The ratio of KH_2PO_4 to $Ca(NO_3)_2$ and KH_2PO_4 to $MgSO_4$ is 48.00, and that of $Ca(NO_3)_2$ to $MgSO_4$ is 1.00.

The lowest yield is shown for culture 4, near the lower right-hand corner of the triangle (see plate 3). The solution supplied to this culture contained the three main salts in the following molecular proportions: 2 percent KH_2PO_4, 80 percent $Ca(NO_3)_2$, and 18 percent $MgSO_4$. Expressed in gram-molecules per liter, the composition of this solution is as follows: 0.0004 M KH_2PO_4, 0.0160 M $Ca(NO_3)_2$, 0.0036 M $MgSO_4$, 0.00001 M $FeSO_4$.

As just mentioned, low yields lie in general on and below a line drawn from the left apex to the middle of the right side of the triangle, while medium and high yields lie above this line. Low yields were not obtained with solutions having partial concentrations of KH_2PO_4 higher than 49 percent of the total molecular concentration, but they were secured with solutions covering the entire tested range (2–96 percent) of partial concentrations of $Ca(NO_3)_2$ and $MgSO_4$.

With respect to the molecular ratios of pairs of the salts, low yields were restricted to solutions having values of the ratio of KH_2PO_4 to $Ca(NO_3)_2$ ranging from 0.02 to 3.00, and thus they appear to be definitely correlated with relatively low values of this ratio. Low yields, however, appear to be independent of the values of the other two molecular ratios, since they were secured with values of KH_2PO_4 to $MgSO_4$ ranging from 0.02 to 24.50 and with values of $Ca(NO_3)_2$ to $MgSO_4$ lying between 0.02 and 48.00.

A medium yield is shown for culture 17, at the center of the triangle, and for all but two of the cultures lying above a line drawn from the left apex to the middle of the right side of the

triangle. Although culture 11 lies in the region generally characterized by medium yields, it gave a low yield; and culture 29, nearest the upper apex, gave a high yield. Medium yields were confined to solutions characterized by partial concentrations of KH_2PO_4 of from 18 to 90 percent, by partial concentrations of $Ca(NO_3)_2$ of from 2 to 33.3 percent, and by partial concentrations of $MgSO_4$ of from 2 to 80 percent. Medium yields therefore seem to be correlated with medium and high concentrations of KH_2PO_4 and with low and medium concentrations of $Ca(NO_3)_2$; but they appear not to be correlated with the partial concentration of $MgSO_4$, except that they were not secured with the two highest tested concentrations of this salt.

For medium yields the ratio values of KH_2PO_4 to $Ca(NO_3)_2$ lie between 1.00 and 40.00, those of KH_2PO_4 to $MgSO_4$ range from 0.23 to 40.00, and those of $Ca(NO_3)_2$ to $MgSO_4$ range from 0.03 to 9.00.

The most conspicuous feature of figure 2 is that the magnitude of the yields of the plants infected with mildew is roughly directly proportional to the ratio of KH_2PO_4 to $Ca(NO_3)_2$ in the culture solution.

Susceptibility to mildew

Wheat plants infected with mildew of course differ in a number of ways from what are regarded as normal plants, and the sum total of these differences constitutes the disease. It has long been known that in the diseased plants the growth rate is less rapid and the final yield is less; the duration of life is shorter; the green color is less intense; the turgor is less (so that the leaves of the diseased plants exhibit a pronounced drooping—see plates 2 and 3); the leaf is overgrown with the fungus mycelium, haustoria penetrate the epidermal cells of the leaf, and tufts of conidia appear in patches on the leaf. Moreover, the rates of metabolic processes (photosynthesis, respiration, digestion, assimilation, etc.) are undoubtedly altered, some being retarded and others accelerated.

In approaching a study of a disease of this sort, it is of course not feasible to investigate all of these differences; attention generally must be confined to one difference or to a few differences, which are selected as indices of the disease. For the purposes of the present paper the difference in dry yields of

infected and uninfected plants has been chosen as the principal index of the disease. Dry yields are easily determined and have the advantage that they lend themselves readily to quantitative treatment. A second index—the approximate amount of fungus spores produced per unit leaf area—is also used here as a rough, indirect measure of the disease.

Susceptibility as indicated by dry yields. In employing the differences in yields as an index of this disease, it is assumed that the yield is always lower for plants infected with mildew than for uninfected plants growing under otherwise similar conditions.[2] The difference in yield between plants infected with mildew and those not thus infected may be used as a measure of the severity of the disease.[3] Indices of the susceptibility to the disease of a number of cultures of wheat may be obtained if the pathogenicity of the mildew is alike for all of the cultures and if a comparison can be made between the dry yields produced in a given period of time by pairs of cultures—one culture of the pair not being infected with mildew and the other culture being infected. The difference in yield between the infected culture and the uninfected culture (this difference being expressed as a percentage of the yield for the uninfected culture) appears to furnish a satisfactory index of susceptibility. If the several pairs of cultures here considered are alike except with respect to the culture solutions employed, the differences in indices of susceptibility may be regarded as related to corresponding differences in the effects of these culture solutions.

Although it was not feasible in the tests here described to grow uninfected cultures simultaneously with the infected cultures, data for the yields of such uninfected cultures have been taken from the results of a similar set of experiments performed at the Johns Hopkins University, in Baltimore, from February 6 to March 6, 1923. A description of these experiments has been published, and the data included in table 2 of

[2] Some cases that cannot readily be distinguished from disease are of course indicated by increased yields. An example is seen in a leguminous plant infected with nodule bacteria. By ordinary criteria portions of the root, at least, are badly diseased, but the plant as a whole grows faster and gives higher final yields.

[3] It is obvious of course that numerical values representing the severity of a disease may differ greatly according to the criteria employed. Thus differences in duration of life may give numerical indices that are quite different from those obtained from dry yields.

the present paper are taken from the published table of results (see Trelease and Livingston, 1924). The general experimental conditions of the former study were similar to those of the present work, the season of the year was the same, and the molecular salt proportions were the same. There were differences, however, in the total concentrations of the solutions—those in the earlier tests varying from 0.0159 M to 0.0273 M (in order to secure a constant initial osmotic value of 1.00 atmosphere for every solution), while the solutions in the later tests all had a molecular concentration of 0.0200 M. Evidence that these differences in total concentration may not be important had been obtained from other tests in which approximately the same growth values were secured with solutions ranging in osmotic value from 0.33 atmosphere to 1.00 atmosphere. The two sets of experiments also differed with respect to the rate of solution renewal—this being 131 cc. per plant per day in the former and 56 cc. per plant per day in the latter. It is clear that the differences between the two sets of experiments allow only tentative conclusions to be drawn from comparisons of the two sets of data.

Table 2 gives a summary of the two sets of experiments. The solution numbers, molecular proportions, and yields of infected plants are the same as in table 1, while the data for the uninfected plants are from the Baltimore tests. The next to the last column of table 2 shows the differences in mean yields between the uninfected plants and the infected plants, and in the last column each difference is expressed as a percentage of the corresponding yield of the uninfected plants.

It will be observed that every solution gave a considerably lower yield when the wheat was infected with mildew than when it was not infected. For each solution the yield obtained when the plants were not infected is here regarded as normal for the kind of plants and general cultural conditions involved. When the plants were infected, the yield was smaller and the difference in yield, expressed as a percentage of the normal yield, is employed as an index of the susceptibility of the plants in this solution (and with the other influential conditions here involved).[4]

[4] The indices of susceptibility represent integrated differences for the time-period of the tests. The values do not allow a study to be made of the manner and degree in which susceptibility may have changed during the experimental period.

TABLE 2

Relation of salt proportions to susceptibility of wheat to injury by mildew infection, as shown by a comparison of top yields of uninfected plants with those of infected plants growing under similar environmental conditions

SOLUTION NUMBER	MOLECULAR PROPORTIONS			TOP YIELDS OF UNINFECTED WHEAT		TOP YIELDS OF WHEAT INFECTED WITH MILDEW		RELATIVE YIELD OF UNINFECTED PLANTS MINUS THAT OF INFECTED PLANTS	ACTUAL YIELD OF UNINFECTED PLANTS MINUS THAT OF INFECTED PLANTS	INDEX OF SUSCEPTIBILITY: DIFFERENCE IN ACTUAL YIELDS AS PERCENTAGE OF YIELD OF UNINFECTED PLANTS
	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	Actual	Relative	Actual	Relative			
				milligrams		*milligrams*			*milligrams*	
6	5	5	90	77.3±1.1	71	39.9±1.1	72	−1	37.4	48
8	5	47.5	47.5	108.5±1.3	100	38.4±0.8	69	31	70.1	65
10	5	90	5	84.7±1.2	78	34.2±0.8	62	16	50.5	60
17	33.3	33.3	33.3	104.2±1.4	96	46.4±0.9	84	12	57.8	55
18	47.5	5	47.5	90.5±1.5	83	45.8±0.9	83	0	44.7	49
19	47.5	47.5	5	82.1±1.2	75	36.7±0.7	66	9	45.4	55
22	50	18	32	108.9±1.2	100	55.4±1.2	100	0	53.5	49
28	90	5	5	88.0±1.1	81	63.2±1.5	114	−33	24.8	28

The values of the indices of susceptibility for the various cultures are interpreted as depending upon the composition of the solutions supplied to the roots. The values given in the last column of table 2 are plotted in the triangular diagram of figure 3, low, medium, and high values being indicated by dots, triangles, and squares, respectively. The culture number is given in paren-

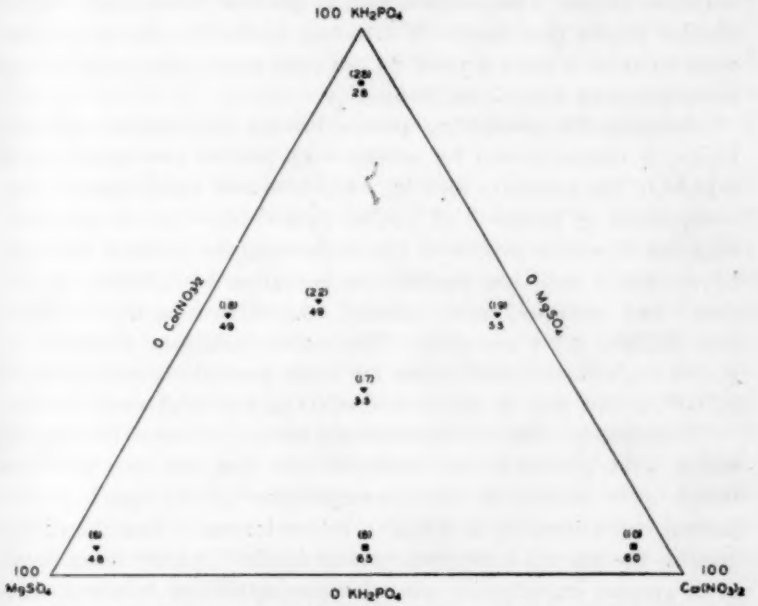

Fig. 3. Indices of susceptibility of wheat to mildew, as shown by dry yields. Culture numbers are above the points representing solutions, and indices of susceptibility are below. Each index represents the difference in dry yields between uninfected and infected cultures, this difference being expressed as a percentage of the yield of the uninfected culture. Low, medium, and high relative values are denoted by dots, triangles, and squares, respectively. Data are from table 2.

theses above each point, and the index of susceptibility is given below.

An examination of figure 3 shows that a low index of susceptibility is indicated for the plants supplied with solution 28 (represented by the point near the upper apex), that high indices are shown for the plants supplied with solutions 8 and 10 (near the middle of the base and near the right apex, respectively), and

that medium values are indicated for the plants of the remaining five cultures.

The pronounced difference between the highest and lowest of the indices deserves special emphasis. The striking difference in the relative susceptibility of the plants receiving these culture solutions is indicated by the fact that the plants supplied with solution 28 gave a mean yield only 28 per cent lower than that of similar plants that were not infected, while the plants supplied with solution 8 gave a yield 65 per cent lower than that of the corresponding uninfected plants.

Solution 28, producing plants having the lowest susceptibility, is characterized by a very high partial concentration of KH_2PO_4 (90 percent) and by very low and equal partial concentrations (5 percent) of $Ca(NO_3)_2$ and $MgSO_4$. In contrast, solution 8, which produced plants having the highest susceptibility, has a very low partial concentration of KH_2PO_4 (5 percent) and medium, equal partial concentrations of $Ca(NO_3)_2$ and $MgSO_4$ (47.5 percent). The other solution, number 10, giving high susceptibility has the same partial concentration of KH_2PO_4, but has 90 percent $Ca(NO_3)_2$ and 5 percent $MgSO_4$.

Perhaps the most conspicuous difference between the solution which gave plants of low susceptibility and the two solutions which gave plants of high susceptibility is the much higher partial concentration of KH_2PO_4 in the former. But the difference in the partial concentrations of $Ca(NO_3)_2$ may be of equal or of greater importance, since low susceptibility is here associated with the solution having a low partial concentration of $Ca(NO_3)_2$ while high susceptibility accompanies medium and high partial concentrations of this salt.

Since the results with only eight sets of salt proportions are shown in figure 3, sufficient information is not available for an adequate correlation of salt proportions and susceptibility. Further studies are needed in order to allow an exact mapping of areas of high, medium, and low susceptibility by the criterion of dry yields; and the results of such studies should allow a more adequate statement of the relations between salt proportions and susceptibility.

The data secured do not warrant a discussion of the nature of the differences in the internal conditions of the plants that are responsible for corresponding differences in susceptibility.

Detailed physiological and morphological studies of diseased and of healthy wheat plants will be required before any evidence will be available on this question. It may be suggested that the plants of low susceptibility might contain greater amounts of potassium and phosphate, and smaller amounts of calcium and nitrate, and might have higher hydrogen-ion concentrations than the plants of high susceptibility; and these differences might, in turn, determine more intricate and as yet little understood physiological conditions that are generally assumed immediately to control susceptibility. Intensive investigation would of course be required before any adequate discussion of these features could be attempted.

Susceptibility in relation to host vigor. For a number of plant diseases caused by obligate parasites, it has been found that a general correlation exists between host vigor and susceptibility to disease—the more vigorous host being more susceptible to such diseases than the less vigorous host (Raines, 1922). It is of interest to examine the present data to see the possible correlations that may exist in the case of wheat mildew under the conditions of these experiments. Table 3 is intended to bring out these relations for the plants supplied with the eight different culture solutions. At the left are shown the vigor classes, high, medium, and low, based upon dry yields of uninfected plants; and at the right are given the corresponding susceptibility classes (as indicated by the percentage difference in growth between infected and uninfected cultures).

It will be noted that plants in the high-vigor class showed high and medium susceptibility; those in the medium-vigor class showed medium and low susceptibility; while those in the low-vigor class showed high and medium susceptibility. These results suggest that a close correlation does not exist between host vigor (as indicated by dry yields of uninfected plants) and susceptibility. The degree of host vigor (as this is influenced by salts supplied to the roots) does not appear to determine the degree of susceptibility to mildew.

Susceptibility as indicated by apparent development of mildew per unit area of host. The relative amounts of mildew spores developed per unit area of the leaves of each culture were scored by comparing the appearance of the cultures. The results of this rating are shown in figure 4, which is similar to figure 1,

but has dots to represent low development of mildew per unit area of the leaves, triangles to represent medium development, and squares to represent high development. On account of the difficulty in making an accurate estimation of this sort by mere observation of the appearance of the cultures, this method has only an approximate quantitative significance.

A comparison of figures 3 and 4 shows that there is a rather good general agreement between the percentage reduction in dry yield and the amount of mildew per unit area of the host.

Low values in figure 4 are indicated for the cultures represented by points along the left margin of the triangle and by

TABLE 3

Susceptibility to mildew (as indicated by percentage difference in dry weight between infected and uninfected cultures) as related to host vigor (as indicated by dry yields of uninfected plants)

VIGOR CLASSES	SUSCEPTIBILITY CLASSES
High	High (culture 8) Medium (culture 17) Medium (culture 22)
Medium	Medium (culture 18) Low (culture 28)
Low	High (culture 10) Medium (culture 6) Medium (culture 19)

two points lying in the upper left-hand corner. The solutions represented by the points nearest to the left margin are those which have a partial concentration of $Ca(NO_3)_2$ of only 2 per-cent—the lowest that was tested. The other two solutions for which low values are indicated (25 and 28) are two of the solutions which have a partial concentration of 5 per cent of $Ca(NO_3)_2$. Low susceptibility is not correlated with the partial concentration of either KH_2PO_4 or $MgSO_4$ alone, since the value of each ranges from 2 to 96 per cent.

By comparing figures 3 and 4, it is seen that solution 28 gave a low value of susceptibility by the two criteria, and that six solutions not included in figure 3 also gave low values. One of

these, solution 25, has 80 percent KH_2PO_4, 5 percent $Ca(NO_3)_2$, and 15 percent $MgSO_4$. The other five have a lower partial concentration of $Ca(NO_3)_2$ than any shown in figure 3. From both of the figures the conclusion is suggested that low susceptibility is correlated with a very low partial concentration (2 percent) of $Ca(NO_3)_2$, or with a slightly higher partial concentration (5 percent) of this salt when the partial concentration of KH_2PO_4 is relatively high (80 percent or 90 percent).

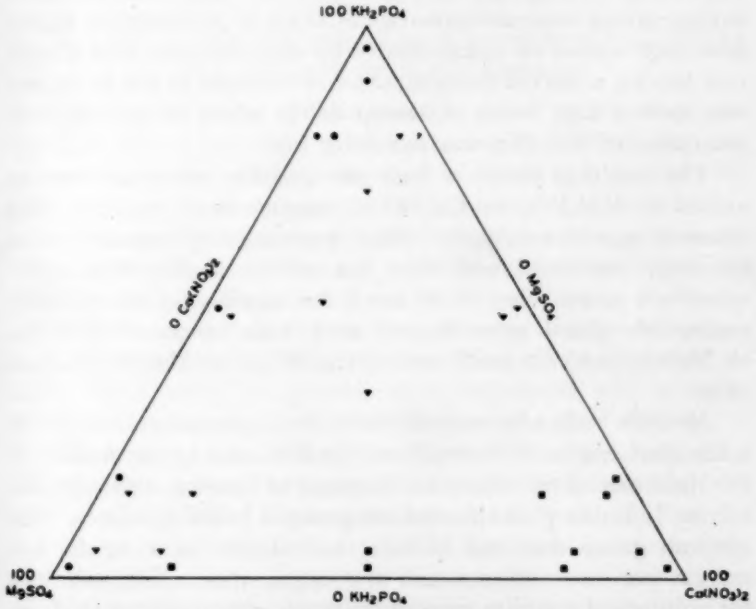

Fig. 4. Susceptibility of wheat to mildew as indicated by the apparent degree of mildew development per unit leaf area. Low, medium, and high relative values are shown by dots, triangles, and squares, respectively.

Turning to the molecular ratios of pairs of the salts, it is found that plants of low susceptibility (as indicated by mildew per unit leaf area) were obtained with solutions having ratio values of KH_2PO_4 to $Ca(NO_3)_2$ ranging from 1.00 to 48.00; these values are thus restricted to the upper part of the total range that was tested. Low susceptibility was limited to the lower part (from 0.02 to 1.00) of the total tested range of ratios of $Ca(NO_3)_2$ to $MgSO_4$. But the values of the ratio of KH_2PO_4

to $MgSO_4$ for low susceptibility range from 0.02 to 48.00, thus covering the entire tested range.

High values of susceptibility are shown in figure 4 for cultures near the lower margin of the triangle and near the right apex. These include eight cultures in addition to the two cultures for which high values are shown in figure 3. The ten cultures are characterized by partial concentrations of KH_2PO_4 ranging from 2 to 18 percent, of $Ca(NO_3)_2$ ranging from 18 to 96 percent, and of $MgSO_4$ ranging from 2 to 80 percent. All tested solutions having partial concentrations of $Ca(NO_3)_2$ of 70 percent or higher gave high values of susceptibility by this criterion, and a solution having a partial concentration of this salt as low as 18 percent gave a high value of susceptibility when the partial concentration of KH_2PO_4 was relatively low.

The fact that plants of high susceptibility were restricted to values of KH_2PO_4 to $Ca(NO_3)_2$ ranging from 0.02 to 0.23 deserves special emphasis. High susceptibility appears to be definitely correlated with very low values of this ratio. The other two ratios seem to be much less significant, since highly susceptible plants were secured with wide ranges of KH_2PO_4 to $MgSO_4$ (0.03 to 9.00) and of $Ca(NO_3)_2$ to $MgSO_4$ (0.23 to 48.00).

Medium values for susceptibility lie in general on and above a line that might be drawn from the left apex to the middle of the right side of the triangular diagram of figure 4, although one culture (number 7) in the medium group is below this line. The medium group does not include the cultures next to the left margin nor two cultures near the upper apex. The solutions for cultures of medium susceptibility are characterized by from 5 to 80 percent KH_2PO_4, from 5 to 49 percent $Ca(NO_3)_2$, and from 2 to 90 percent $MgSO_4$. The molecular ratios of KH_2PO_4 to $Ca(NO_3)_2$ for this group range from 0.33 to 9.50, those of KH_2PO_4 to $MgSO_4$ lie between 0.06 and 40.00, and those of $Ca(NO_3)_2$ to $MgSO_4$ are between 0.06 and 24.50.

In general, the results presented in figure 4 suggest that low susceptibility is restricted to cultures having relatively very high values of the ratio of KH_2PO_4 to $Ca(NO_3)_2$, and that the susceptibility becomes greater as the ratio of KH_2PO_4 to $Ca(NO_3)_2$ becomes smaller.

Since only one variety of wheat was used, the present study

gave no information concerning the relative degrees of susceptibility of various varieties of wheat to the strain of mildew employed. If a number of varieties of wheat were ranked in the order of susceptibility to a certain strain of mildew with one soil or fertilizer combination, it might not be possible to alter this ranking by the use of another fertilizer combination. Although the susceptibility of each variety may be influenced, this might be done without changing the order of the several varieties.

AN ANALYSIS OF THE CONDITIONS THAT DETERMINE THE NATURE AND SEVERITY OF PLANT DISEASE

The present study of the influence of salt nutrition on the susceptibility of wheat to mildew has emphasized the extreme complexity of the system composed of the host plant infected with a parasite. Many variable conditions are of course effective within this system, and these internal conditions are profoundly influenced by the environment. For an understanding of the general principles determining the kinds and degrees of physiological derangements that constitute disease, detailed investigation of many phases of the general problem will be required. It seems worth while to analyze, in a preliminary way at least, the general complex of conditions that control plant disease.

The nature and severity of a plant disease resulting from infection by a parasite are generally thought of as determined by (1) the susceptibility of the host, or the sum total of all of the conditions of the host that tend to facilitate injury by the parasite; (2) the pathogenicity of the parasite, or the summation of the conditions of the parasite tending to promote injurious action on the host; and (3) the length of the time-period during which the parasite acts on the host.

The susceptibility of the host is regarded, from the experimental point of view, as determined by the nature and size[5] of

[5] The significant features in the nature of the host that determine degree of susceptibility are of course unknown at the present time. They are supposed to be certain morphological and physiological conditions normally present in the host or developing in response to conditions that usually accompany invasion by the parasite. Working hypotheses that have proved very useful in animal pathology are discussed by Zinsser (Infection and resistance. 666 p. New York: The Macmillan Co. 1923).—The size of the host is important in so far as it affects the mass relations between host and parasite.

the host; and these characteristics are considered to depend, in turn, upon the genetic constitution and phase of development (or age) of the host, and the complex of environmental conditions influencing the host before infection and during the development of the disease. Similarly, the pathogenicity of the parasite is considered to be controlled by the nature and mass (volume, number, etc.) of the parasite acting on the host; and these features of the parasite, in turn, depend upon the genetic makeup and the phase of development (or age) of the parasite, and the complex of environmental conditions affecting the parasite before and during its association with the host.

In order to obtain an idea of the various degrees of susceptibility of a number of different host plants, the pathogenicity of the parasite and the length of the time-period during which the parasite acts on the host are controlled or maintained alike for all the hosts. The host plants whose suceptibility is studied may be of different genetic strains, they may be of different phases of development (or ages), they may have been subjected to different environmental complexes, or they may differ with respect to several of these features. If a number of hosts differing in any of these respects are equally inoculated with the same parasite (for example, with an equal number of spores per unit area of host) and if the pathogenicity of the parasite is kept the same for all hosts, the nature and severity of the disease which develops in each host in a given time-period is taken as an index of the corresponding susceptibility of each host. In some studies susceptibility is considered as being proportional to the reciprocal of the time-period required for the development of a standard degree of disease under uniform conditions.[6] To have each of the uncontrolled influential conditions the same for all cultures, the tests usually are conducted simultaneously; or if they are carried on at different times, these influential conditions are kept essentially alike in the various tests. This is

[6] Susceptibility might also in some cases be considered as inversely proportional to the mass of the parasite per unit mass of host needed to bring about a standard degree of disease in a given time-period.

In view, however, of the minuteness of the amounts of toxins and antibodies concerned in the phenomena of certain diseases and in general the relative permanence of enzymes during and after the changes which they accelerate, such considerations of time and mass may have relatively little significance.

necessary since indices of susceptibility are regarded as dependent upon the general complex of conditions that are effective upon host and parasite before and during the development of the disease. Thus, indices of susceptibility may be expected to depend upon environmental conditions, the mass relations of parasite and host, etc.

To obtain information concerning the various degrees of pathogenicity of a number of parasites, the susceptibility of the host and the time-period during which the parasites act on the host are kept alike for all of the parasites. Thus, if several different parasites (differing in species or strain, developmental phase, previous environmental conditions, etc.) are used to inoculate similar hosts (the proportions of parasite to host preferably being constant), and if the susceptibility of these hosts is maintained uniform, then the nature and severity of the disease resulting from each parasite in a standard time period is taken as an index of the corresponding pathogenicity of each parasite. Or the index is considered as proportional to the reciprocal of the time-period required to produce a standard degree of disease.[7] The tests are generally made simultaneously, in order to insure uniformity of influential conditions; or these conditions are maintained effectively alike in tests made at different times. This is important because the values of such indices are known to be influenced by the environmental complex, the mass relations between parasite and host, etc.

The pronounced effects which environmental conditions may produce upon the susceptibility of plants to disease has become increasingly evident from many recent investigations. Although sufficient information is not yet available for discussing adequately this phase of the general subject of the control of plant disease, it seems worth while to attempt here to list briefly some of the most important of these environmental conditions.[8] The

[7] From another point of view, the index may be regarded as inversely proportional to the mass of the parasite per unit mass of host required to bring about a standard degree of disease in a given time-period.

[8] Even an enumeration of these conditions is confused by incompleteness of our present knowledge—for example, by our inability so far to distinguish qualitatively between the action of temperature as a normal condition for maintenance of life and its action as a stimulus in the technical sense (*i.e.*, an agency which releases energy manifestations of far greater magnitude than would be expected from the apparent energy value of the agency itself).

environmental conditions that may influence the susceptibility of the host may, for convenience, be analyzed into two groups —those which act on the aerial parts and those which affect the roots. It is convenient to divide these influential aerial conditions into physical conditions and chemical conditions. The physical conditions include the temperature and water evaporating power of the air; the quality and intensity of light and of other forms of radiant energy; the velocity of the wind; and the nature and rate of precipitation, of rain, hail, sleet, dust and smoke particles. The chemical conditions that may be of special importance are the carbon-dioxide supplying power (depending upon concentration of carbon dioxide in the atmosphere near the plant, rate of diffusion, rate of air movement); the oxygen supplying power; and, rarely, the power of the air to supply various other substances, such as sulphur dioxide, sulphuric acid, illuminating gas, smoke, etc. Fungicides, applied by man, should be mentioned in this connection, owing to their great importance in the "control" of disease; however, their influence is mainly to inhibit the pathogenicity of parasites.

The environmental conditions acting upon the roots of the host and tending to influence its susceptibility may be classified, as are the aerial conditions, into physical and chemical conditions.[9] The physical conditions that usually are effective are the temperature of the solution or the soil; the osmotic value of the solution surrounding the roots; the water-supplying power of the medium; and the mechanical properties of the medium—these being especially important in ordinary soils, where solid, liquid, and gaseous phases exist. The important chemical conditions are the kinds of solutes in the solution around the roots (nutritive, toxic, stimulating, etc.), including mineral salts, organic substances, dissolved gases (especially oxygen and carbon dioxide), hydrogen and hydroxyl ions, etc.; the supplying power of each kind of solute to the root surface, depending upon the concentration of each solute in the solution, the rate of mass movement of the solution, and the rate of diffusion of the solute; and the relative proportions or "balance" of solutes.

[9] Biological conditions (comprising kinds and numbers, per unit soil volume, of bacteria, fungi, algae, protozoa, etc.) may for convenience be considered a third group. These act, of course, through modifying physical and chemical conditions. A similar group of biological conditions may be considered in connection with aerial conditions.

The relation of any one of these environmental conditions to susceptibility and pathogenicity may be expected to depend not only upon the nature of the environmental condition in question but also upon the whole complex of other influential conditions of the host, of the parasite, and of the environments of each. This statement does not imply that all of the features here considered have equal quantitative significance. Sufficient study may indeed show that a relatively small number of these conditions generally exert such a preponderating influence that the combined effects of the other conditions may be regarded as negligible.

SUMMARY

Marquis wheat was grown in twenty-nine different culture solutions, every solution having a total molecular concentration of 0.02 gram-molecule per liter and the various solutions giving a wide range of proportions of the three main salts—KH_2PO_4, $Ca(NO_3)_2$, and $MgSO_4$. Each solution contained 0.00001 gram-molecule of $FeSO_4$ per liter. When the first leaf had expanded, the cultures were heavily inoculated with spores of mildew (*Erysiphe graminis*). Notes were made of the appearance of the plants, and at the end of 31 days growth the plants were harvested and their dry weights were determined. Comparison of infected cultures growing in eight of the solutions with uninfected plants growing in solutions of approximately the same composition allowed a study to be made of the relative degrees of susceptibility as this was related to the salt solutions supplied to the roots.

The principal index of susceptibility employed for plants grown in eight of the solutions was the difference in yields between uninfected plants and infected plants growing in solutions of nearly the same composition and under similar environmental conditions, this difference being expressed as a percentage of the yield of the uninfected plants. For plants growing in all of the twenty-nine solutions, the apparent development of mildew per unit area of the host was also employed as an index of susceptibility.

Pronounced differences in susceptibility were found to exist between plants supplied with different culture solutions. Thus, the susceptibility of Marquis wheat to mildew may be influenced

to a high degree by the composition of the culture solution supplied to the roots.

On the basis of dry yields, the least susceptible plants were secured with a solution having the following molecular proportions of the main salts: 90 percent KH_2PO_4, 5 percent $Ca(NO_3)_2$, and 5 percent $MgSO_4$ (total concentration, 0.02 gram-molecule per liter). The most susceptible plants were those supplied with a solution containing 5 percent KH_2PO_4, 47.5 percent $Ca(NO_3)_2$, and 47.5 percent $MgSO_4$ (total concentration, 0.02 gram-molecule per liter).

Judging by the development of mildew per unit leaf area, the plants supplied with 96 percent KH_2PO_4, 2 percent $Ca(NO_3)_2$, and 2 percent $MgSO_4$ (total concentration, 0.02 gram-molecule per liter) were even less susceptible than those given 90 percent KH_2PO_4 and 5 percent of each of the other salts. By the same criterion the plants grown in several other solutions having very low partial concentrations of $Ca(NO_3)_2$ were also in the group of low susceptibility.

The dry yields of the infected plants were greatest in the solution having the following molecular proportions of the three main salts: 96 percent KH_2PO_4, 2 percent $Ca(NO_3)_2$, and 2 percent $MgSO_4$ (total concentration, 0.02 gram-molecular per liter). The salt proportions that allowed approximately optimum growth of the infected plants are different from those which permitted approximately optimum growth of the uninfected plants.

Host vigor and susceptibility to mildew appear not to be closely correlated, under the conditions of the present tests and by the criteria here employed. Some of the plants of high vigor (as shown by high dry yields of uninfected cultures) were of high susceptibility, while others were of medium susceptibility; plants of medium vigor ranged from medium to low in susceptibility; those of low vigor were of medium and high susceptibility. Thus, some condition, or conditions, that may be independent of vegetative vigor appear to determine the susceptibility of the host. It may be noted that these experiments give no support to the view that low vigor of the host is an index of its high susceptibility to invasion by a parasite.

The conclusions that may be drawn from these tests must be regarded as applying only to the particular experimental con-

ditions involved in these studies. Indices of susceptibility may be expected to depend upon the general complex of influential conditions.

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NEW YORK CITY

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Description of plates

The photographs of plates 2 and 3 show cultures of wheat plants 28 days after initial infection with mildew. The various cultures were supplied with solutions containing KH_2PO_4, $Ca(NO_3)_2$, and $MgSO_4$ in different molecular proportions; every solution also contained 0.00001 M $FeSO_4$. See table 1.

PLATE 2

Cultures 8 and 10 have a high index of susceptibility to mildew; cultures 6, 17, 18, 19, and 22 have medium indices of susceptibility; and culture 28 has a low index of susceptibility. See also table 2 and figure 3.

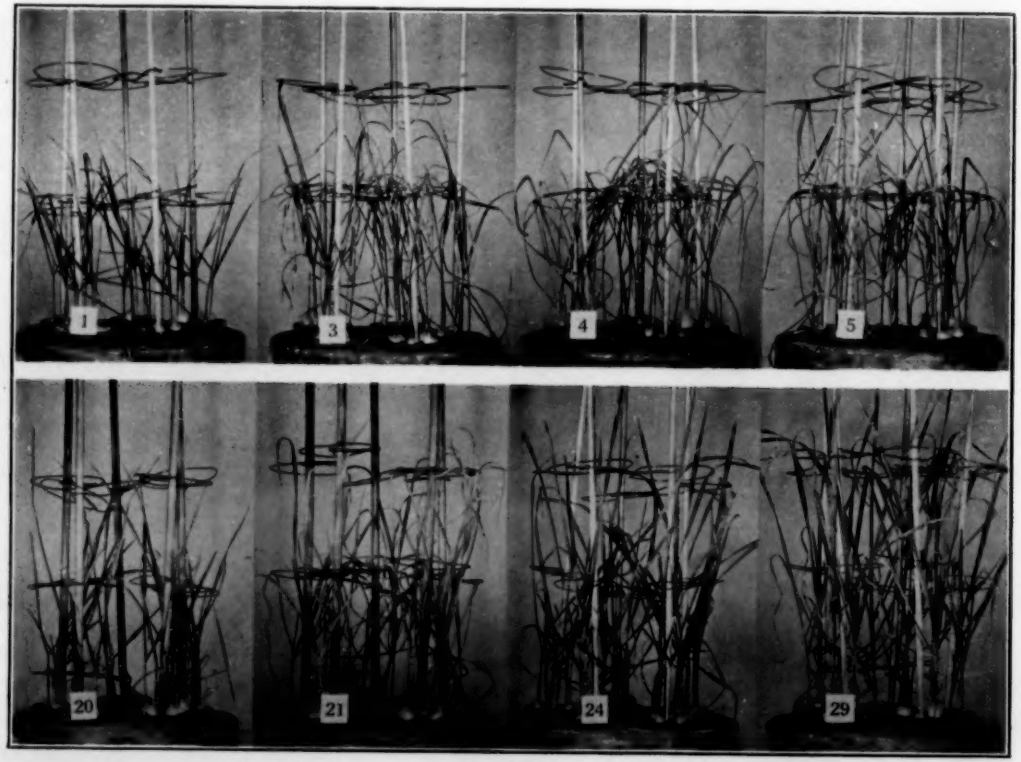
Cultures 6, 8, 10, and 19 gave low relative dry yields; and cultures 17, 18, 22, and 28 gave medium relative dry yields. See also table 1.

PLATE 3

Cultures 3, 4, and 5 are of high relative susceptibility; culture 21 is of medium relative susceptibility; and cultures 1, 20, 24, and 29 are of low relative susceptibility. See also figure 4.

Cultures 1, 3, 4, 5, and 21 gave low relative dry yields; cultures 20 and 24 gave medium relative dry yields; and culture 29 gave a high relative dry yield. See also table 1.

WHEAT MILDEW



WHEAT MILDEW

Callisteris violacea Greene

WILLIAM A. DAYTON[1]

(WITH PLATE 4)

By letter of January 22, 1914, Dr. Coville returned to the Forest Service the remaining plants (the non-grasses) of our '2d Montezuma Collection,' our serial nos. 11532 to 11563, inclusive. These plants were collected, mainly if not entirely in 1913, by unknown collectors on the Montezuma National Forest in southwestern Colorado. With these specimens Dr. Coville returned the empty folder of collector's no. *15*, our serial no. 11544, which had this notation on it in the hand of the late Dr. E. L. Greene (who at that time was consulting expert of the Forest Service in matters of plant identification):

> The content of this folio is a new species of the genus *Callisteris* soon to be published and the specimens retained.

Later in the memorable year of 1914 the following description of a new *Callisteris* appeared (in Repert. Spec. Nov. **13**: 324):

> CALLISTERIS VIOLACEA Greene, spec. nov. Caules e radice perenni usque 3-4 dm. alti, undique parce puberuli. Folia pinnatisecta subglabra. Calyx fere usque ad basim 5-partitus, laciniis subulato-linearibus apice insigniter attenuatis, undique pube brevissima subglandulosa obsitus. Corolla 3 dm. (*cm.* evidently intended—W.A.D.) longa, anguste tubiformis, tubo tenui violaceo, limbo 1.5 cm. lato, puniceo, laciniis ovato-lanceolatis tenuissime acuminatis. Capsula ignota.
>
> Montezuma National Forest, Colorado, 1913. Specimens sent by some one employed in the Forest Service of the United States whose name is not given. While the basal foliage is wanting, the very deeply cleft calyx with its long almost caudately acuminate segments, no less than the long slender violet corolla-tube, marks it as a species not before known.

Dr. Greene, it will be noted, failed to state where the type specimen was deposited. Such a specimen was not to be found in the type collection of the United States National Herbarium nor is there any specimen labeled *Callisteris violacea* in the main collection of that institution. Neither the Forest Service's Washington office, nor the District Forester's office at Denver,

[1] In charge forage investigations, office of Range Research, U. S. Forest Service.

nor the Montezuma Supervisor's office at Mancos, Colorado, has a specimen of serial no. 11544 nor one labeled *Callisteris violacea*. Inquiry of Dr. J. A. Nieuwland of the University of Notre Dame, where Dr. Greene's botanical library and herbarium are now located, developed that this specimen is not there.

One day last summer, on going hurriedly through the National Herbarium *Gilia* collection with another purpose in mind, my attention was attracted to a specimen in a *Gilia aggregata* folder, a photograph of which is shown herewith (PLATE 4). Examination of it has left no doubt in my mind that it is the lost type of *Callisteris violacea* Greene. My reasons for this view are:

1. The type of *Callisteris violacea* came from the Montezuma National Forest, and was collected there in 1913 by some unknown officer of the Forest Service.

2. U. S. National Herbarium specimen no. 583367 (figured herewith) was collected by some anonymous person on the Montezuma National Forest in 1913.

3. No. 583367 is the only *Gilia* from the Montezuma National Forest in the U. S. National Herbarium.

4. The records of the Forest Service indicate that a specimen of *Gilia*, collector unknown, collector's no. *15*, Washington office no. 11544, was collected in 1913 and was retained by the late Dr. Greene with the statement that it was new and soon to be published.

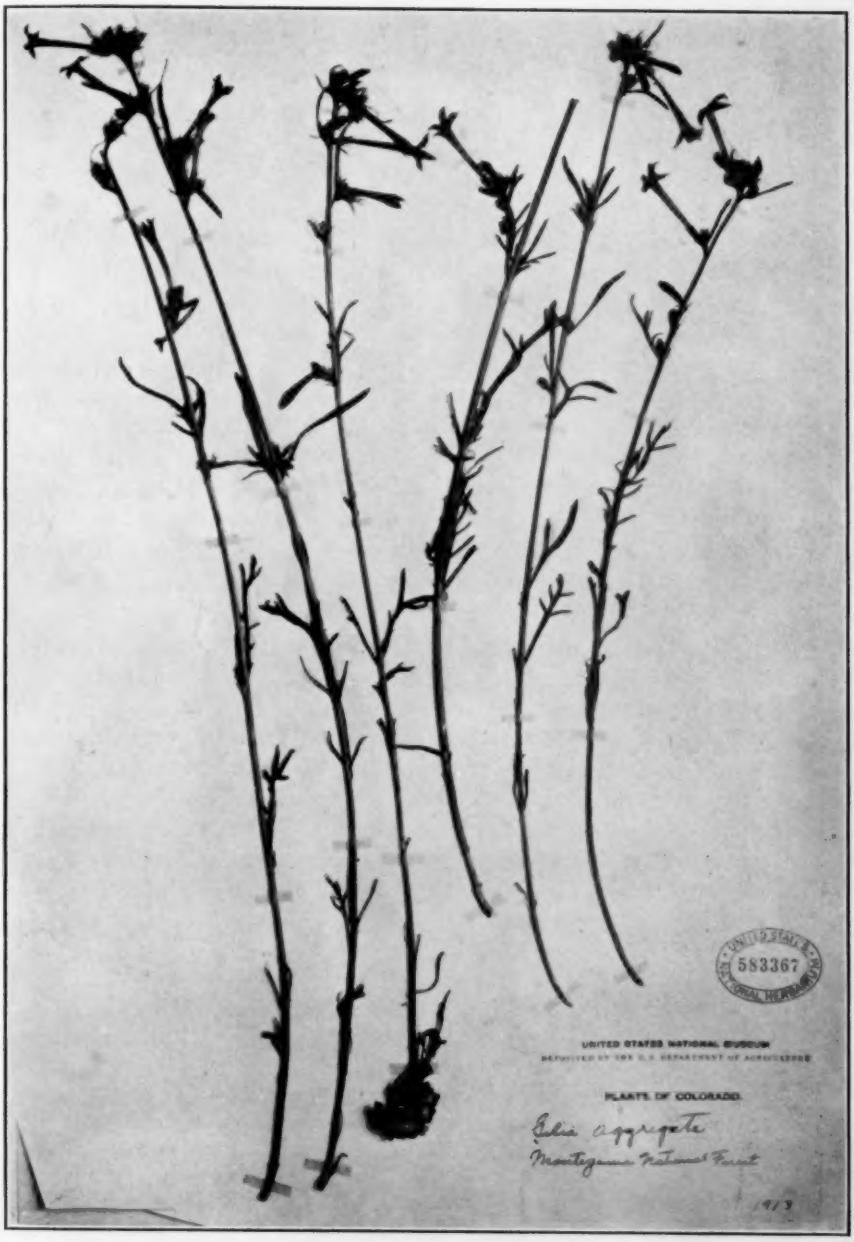
5. The records of the Forest Service further indicate that only one specimen of *Gilia* from the Montezuma National Forest (that mentioned above) was ever retained by Dr. Greene (and presumably for later deposit in the U. S. National Herbarium).

6. The description of *Callisteris violacea* aptly applies to U. S. National Herbarium specimen no. 583367.

The conclusion appears irresistible that U. S. National Herbarium specimen no. 583367 is Forest Service specimen no. 11544 and the type of *Callisteris violacea* Greene. A statement of these facts has been presented to Dr. W. R. Maxon, and recommendation made to him that this specimen be deposited in the type collection of the National Herbarium as the type of *Callisteris violacea* Greene.

Few American botanists of the present day appear to regard *Callisteris* as a valid genus. *Callisteris violacea* Greene (which should not be confused with the very different, Californian

Gilia violacea Heller) seems pretty clearly to be a synonym of *Gilia aggregata* (Pursh) Spreng., though possibly some might think there is enough white-hairiness on calyces and pedicels to place the specimens in *Gilia pulchella* Dougl. The writer would certainly place them, as Mr. Standley has done already, in *G. aggregata*. The accompanying photograph hardly shows it, but the deep division of the calyx which Dr. Greene emphasized in his description, while generally characteristic of these particular specimens, is a variable character, for the same plant shows calyces split almost to the base and also some that are cleft not much more than halfway. This character varies too with age, as the calyx naturally tends to become increasingly scarious (and hence liable to part) between the lobes with advancing maturity.



TYPE SPECIMEN OF CALLISTERIS VIOLACEA GREENE

A new Gilia from the Montezuma National Forest

WILLIAM A. DAYTON[1]

(WITH PLATE 5)

In 1922 Mr. Frank H. Rose, at that time an officer of the U. S. Forest Service but now chief warden of the National Bison Range, Bureau of Biological Survey, Moiese, Montana, made an extensive collection of plants on the Montezuma National Forest, Montezuma and LaPlata Counties, southwestern Colorado. Among these specimens is Mr. Rose's no. *R-102*, our Washington office serial no. 40183, illustrated herewith (PLATE 5) which neither Mr. Ivar Tidestrom, consulting expert of the Forest Service in matters of plant identification, nor I could run down in any of the keys. Mr. Tidestrom thought it might be Dr. Greene's *Callisteris violacea*, the type of which came from the Montezuma Forest and labeled the specimen tentatively as *Gilia violacea* (Greene) . . . Mr. Tidestrom's attention, however, was then called to the earlier *Gilia violacea* Heller (Muhlenbergia 1: 56. 1904), a small-flowered Californian annual, and we agreed between us to name this specimen *Gilia Montezumae* Tidestrom & Dayton, but the name was never published although it appears in our Forest Service plant lists.

Since the identity of *Callisteris violacea* Greene has now been cleared up (see preceding paper) and that is shown to be an entirely different plant from Mr. Rose's no. *R-102*, it is now feasible to publish a diagnosis of the latter specimen as the type of a hitherto undescribed species.

Gilia Montezumae Tidestrom & Dayton, sp. nov.

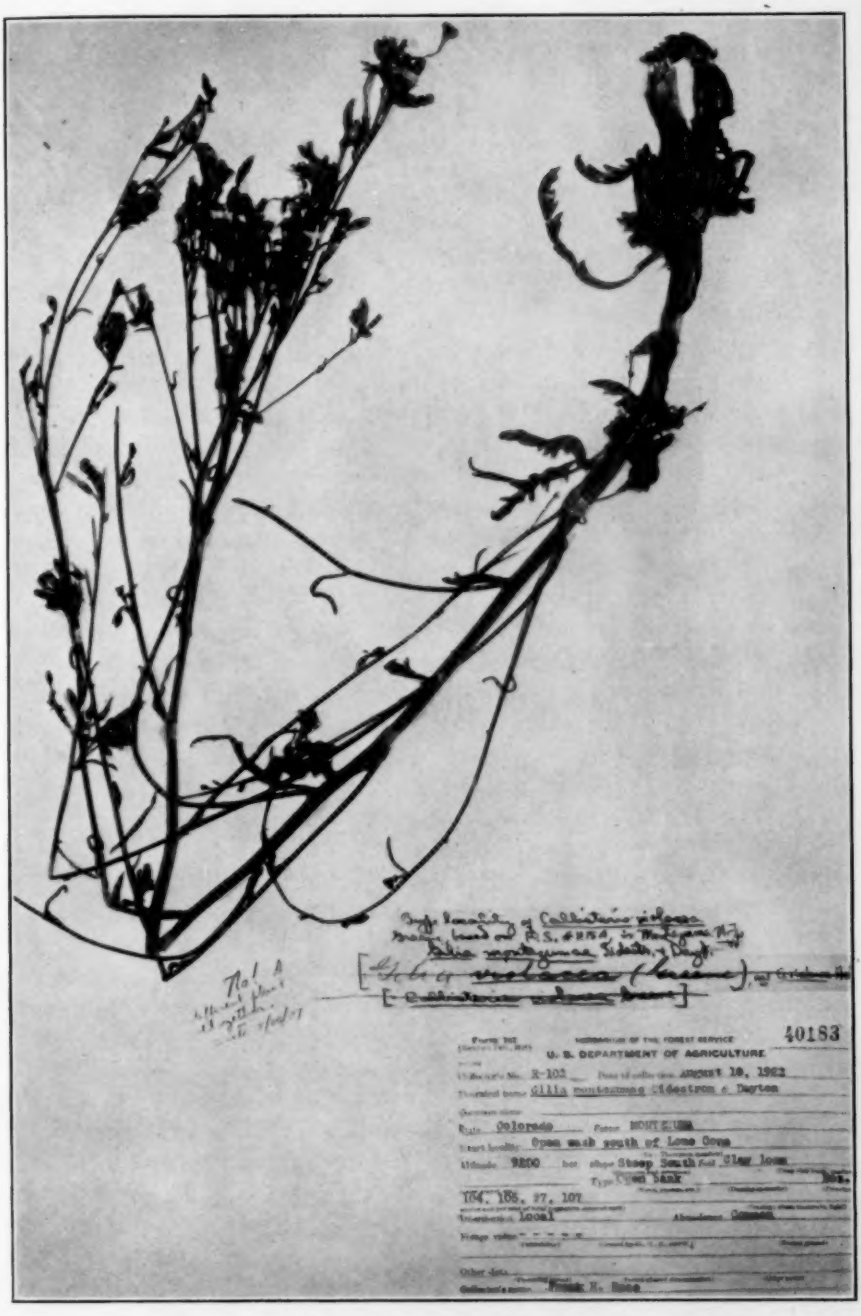
Herba biennis, vel forsan breviperennis, unicaulis paene e basi gracili-ramulosa, 30–55 cm. alta, praeter in inflorescentia nequaquam glandulosa. Folia plus minusque puberulenta; inferiora pinnatifida, laciniis lanceolatis cuspidatis 2–8 mm. longis; superiora diminuta. Paniculum patulum multiflorum; pedicella brevia glandulosa; calyx glandularis 5–7 mm. longa, lobis anguste lanceolatis non raro quam tubus brevioribus; corolla

[1] In charge forage investigations, office of Range Research, U. S. Forest Service.

purpurea tubulari-infundibuliformis 15–24 mm. longa, tubo sparsim puberulento quam calyx bis terque longiore, limbo angusto, nonnunquam 7 mm. lato.

Apparently biennial, perhaps brief-perennial; stem stout solitary, branching near the base, about 30–55 cm. high, mostly bright green though more or less stained with purple especially at the base and in the inflorescence, smooth, beset with a sparse short soft somewhat chaffy and crisp puberulence. Leaves more or less puberulent, especially the ones in the basal rosulate tuft; basal and lower stem leaves 5 to 8 cm. long, pinnatifid, the lobes 2–8 mm. long, lanceolate, mostly cuspidate; uppermost leaves reduced, linear or nearly so, entire or nearly so, passing gradually into small bracts. Inflorescence many-flowered, elongated, loose, open, of often rather congested about 10-flowered corymboid clusters paniculately disposed; pedicels glandular, about 3 mm. long; calyx glandular, often purplish, 5–7 mm. long, the teeth narrowly lanceolate, usually shorter than the tube; corolla purplish, tubular-funnelform, 15–24 mm. long, the tube somewhat puberulent, gradually tapered downwards, about two or three times longer than the calyx, the limb about 5–7 mm. broad with rounded-obovate, often mucronate lobes. Capsules about 6–8 mm. long; seed not seen.

Type (to be deposited in U. S. National Herbarium), *Frank H. Rose R-102*, Forest Service serial no. 40183, collected August 18, 1922, Montezuma National Forest, Colorado, at 9200 ft., steep south slope, open bank of wash south of Lone Cone, common but local, associated with *Chaenactis Douglasii*, *Eriogonum lonchophyllum*, *Lychnis striata*, and *Mentzelia multiflora*. Duplicates of the type are on file in the herbarium of the District Forester at Denver and of the Montezuma National Forest Supervisor at Mancos, Colorado.



GILIA MONTEZUMAE TIDESTR. & DAYTON: TYPE SPECIMEN

UNIV OF MICH

New plants from Colorado

GEORGE E. OSTERHOUT

Quamoclidion cordifolium sp. nov. Stems stout, spreading or ascending, glabrous below, densely and finely pubescent near the top and on the peduncles; the upper-most leaves rounded at the base, shortly pointed at the apex, 5–7 cm. wide, 6–8 cm. long, on very short petioles, the lower leaves rounded at the apex, cordate at the base, about 12 cm. wide, 10 cm. long, petioles 2–3 cm. long: the larger involucres 3.5 cm. high, the bracts united for 2 cm., and rounded but with a short point, densely and finely pubescent, the involucre 6 flowered, the expanded perianth 6–6.5 cm. long, its tube 4–4.5 cm. long, green, with heavier veins and pubescent below, the limb purple, 3–3.5 cm. wide in the pressed flowers; the fruit narrowly ovate, 10 mm. long with 10 or 12 slender ribs, pubescent.

Collected some six miles from Grand Junction, in the hills across the Colorado River, 18 June 1926; *no. 6559*.

Astragalus linifolius sp. nov. (**Ctenophyllum linifolium** sp. nov.) Stems many from a thick woody root, much branched, glabrous below, somewhat strigose above, 4–6 cm. high; stipules small and scarious; leaves very slender, almost filiform, 6–10 cm. long, only occasionally with a small leaflet or a pair of small leaflets; peduncles 2 cm. long or more, bearing 4–8 racemose flowers, the flowers white, the banner rather slender, 15 mm. long, the keel 12 mm. long with a small purple tip, the pubescent calyx 5 mm. long, and the slender teeth 2 mm. long; the sessile pod 15 mm. long, almost round in cross section, 5–6 mm. in diameter, both sutures prominent, but neither intruded, cross-wrinkled, but not strongly so.

Collected in the hills some six miles across the Colorado River from Grand Junction, 18 June 1926; *no. 6557*.

Astragalus linifolius is close to *A. rafaelensis* Jones, and may be a variety of that species. *A. rafaelensis* comes from Woodside, Utah.

Townsendia diversa sp. nov. Many stemmed from a stout perennial tap-root, the stems dividing below the surface and spreading, 3–6 cm. long, the leafy portion only 2–4 cm. high,

canescent, almost concealed by the numerous spatulate, canescent leaves, these about 10 mm. long, including the petiole of 4 mm.; the heads of flowers numerous, terminating the short stems, about 8 mm. wide, and the bracts in three series, 7 mm. long, strigose-pubescent, the margins scarious and fimbriate-ciliate, often reddish; the rays lilac, about 10 mm. long; the achenes 3 mm. long, thinly pubescent, the pubescence capitellate; the pappus of the disk achenes 4 mm. long, that of the ray achenes none, or only a fringe made by the hairs of the achenes.

Perhaps this is nearest to *Townsendia strigosa* Nutt., but that is said to be a biennial or winter annual, and the achene of the ray flowers has a crown of short squamellae.

Collected in the hills across the Colorado River from Grand Junction, 31 May 1921; *no. 6116*.

Senecio taraxacoides nudatus var. nov. Perennial from a strong rootstock, with spreading rootlets, the stem 6–10 cm. high, slightly tomentose, bearing one or two heads at the top, the leaves mostly basal, 4–6 cm. long including the petiole, spatulate and dentate, slightly tomentose; the heads of discoid flowers often recurved, 10–15 mm. broad, the brown bracts 8–10 mm. long, acuminate and somewhat scarious on the margins, the flowers yellow, the achenes glabrous.

Collected on Specimen Mountain, on the line of Larimer and Grand Counties, 19 August 1926; *no. 6650*.

ABRONIA GLABRIFOLIA Standley. The writer collected this peculiar *Abronia* near Grand Junction, Mesa County, 19 June 1926. Dr. Edwin B. Payson has also collected it in the vicinity of Montrose, Montrose County.

SALVIA SYLVESTRIS L. There is a well established bunch of this *Salvia* growing in an uncultivated field south of Dale Creek, Larimer County. Dr. I. M. Johnston of the Gray Herbarium identified a specimen for me.

WINDSOR, COLORADO

INDEX TO AMERICAN BOTANICAL LITERATURE
1926–1927

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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